
SYSTEMATIC COMPARISON AND SOME BIOLOGICAL CHARACTERISTICS OF RHIZOPHORACEAE AND ANISOPHYLLEACEAE¹

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ABSTRACT

Systematic and biological characteristics of Rhizophoraceae and Anisophylleaceae are detailed. Comparison of a wide variety of vegetative and reproductive characters reveals virtually no points of agreement between the two families. Characters such as the basically diplostemonous androecium are of such wide occurrence in choripetalous dicotyledons as to be phylogenetically insignificant. One apomorphy found in both families, divided or appendiculate petal margins, occurs in several unrelated families also and is judged to be a homoplasy. Cladistic analysis of Rhizophoraceae shows that, not surprisingly, information now in hand about most Malesisae is inadequate to resolve the relationships of the genera and clades of this tribe. The remainder of the proposed phylogenetic tree is very robust and shows that, as traditionally circumscribed, tribe Gynotrocheae is paraphyletic. Carallia is evidently the inland genus most closely related to the mangroves. Bruguiera, although characterized by several remarkable autapomorphies, is the most primitive of the mangrove genera, and Rhizophora is the most derived.

The Rhizophoraceae (used sensu stricto throughout this article) and Anisophylleaceae have often been treated as a single family, although some recent phylogenetic treatments of the angiosperms have placed them separately (Cronquist, 1981; Dahlgren, 1980), as originally suggested by Ridley (1922). We believe that this lack of consensus stems largely from the absence of detailed information on a wide variety of systematic characters of the two families, rather than from differences in interpretation. Detailed discussions of several specific suites of characters, such as pollen and leaf architecture, appear elsewhere in this volume, so we have emphasized other, mostly morphological, characters that are either not widely understood for these two families or not generally considered in systematic comparisons. A summary of the systematic differences between Rhizophoraceae

and Anisophylleaceae in these characters forms Table 1.

Despite the fact that most botanists are somewhat familiar with the mangrove Rhizophoraceae, particularly the genus *Rhizophora*, the biology of these plants is widely misunderstood. Accordingly, in a second section of this article, we discuss some of the biological adaptations to the mangrove habitat that are found in Rhizophoraceae, with as much comparative reference to the inland genera as the current state of our knowledge permits.

SYSTEMATIC COMPARISON

DISTRIBUTION AND HABITAT

Rhizophoraceae and Anisophylleaceae are tropical families of shrubs and trees; only a few species of mangrove Rhizophoraceae stray beyond 22° lat-

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FIGURES 1, 2. Aerial roots of mangrove Rhizophoraceae. Localities given in parentheses.—1. Stilt roots of *Rhizophora harrisonii* (Costa Rica).—2. Stilt and knee roots of *Bruguiera gymnorhiza* (Queensland). Development of knee roots is illustrated in Figure 29.

itude, and then only on coastlines with warm currents. Taxa of both families occur in most of the major moist-tropical floristic regions. The preponderance of genera with only one or two species and the narrow geographic ranges of those genera (Juncosa & Tomlinson, this volume) suggest that both may be relictual families.

For its size, the Rhizophoraceae have an exceptionally wide ecological and geographic range. The mangrove taxa are found on virtually all tropical coasts, and inland species grow in many moist forest types, both primary and successional. A few species, mostly in the genus *Cassipourea*, grow in drier habitats. Several genera of Rhizophoraceae (both inland and mangrove) may form very large trees (to 50 m), but most species are small trees and may begin flowering at heights of only 1–2 m.

Anisophylleaceae are characteristically large trees of wet lowland primary forest, although the genus *Anisophyllea* also includes some elegant small shrubs (e.g., *A. disticha*). *Combretocarpus* is a dominant tree of Bornean (fresh water) peat swamp forest, apparently now extinct in peninsular Malaysia (F. S. P. Ng, pers. comm., 1981).

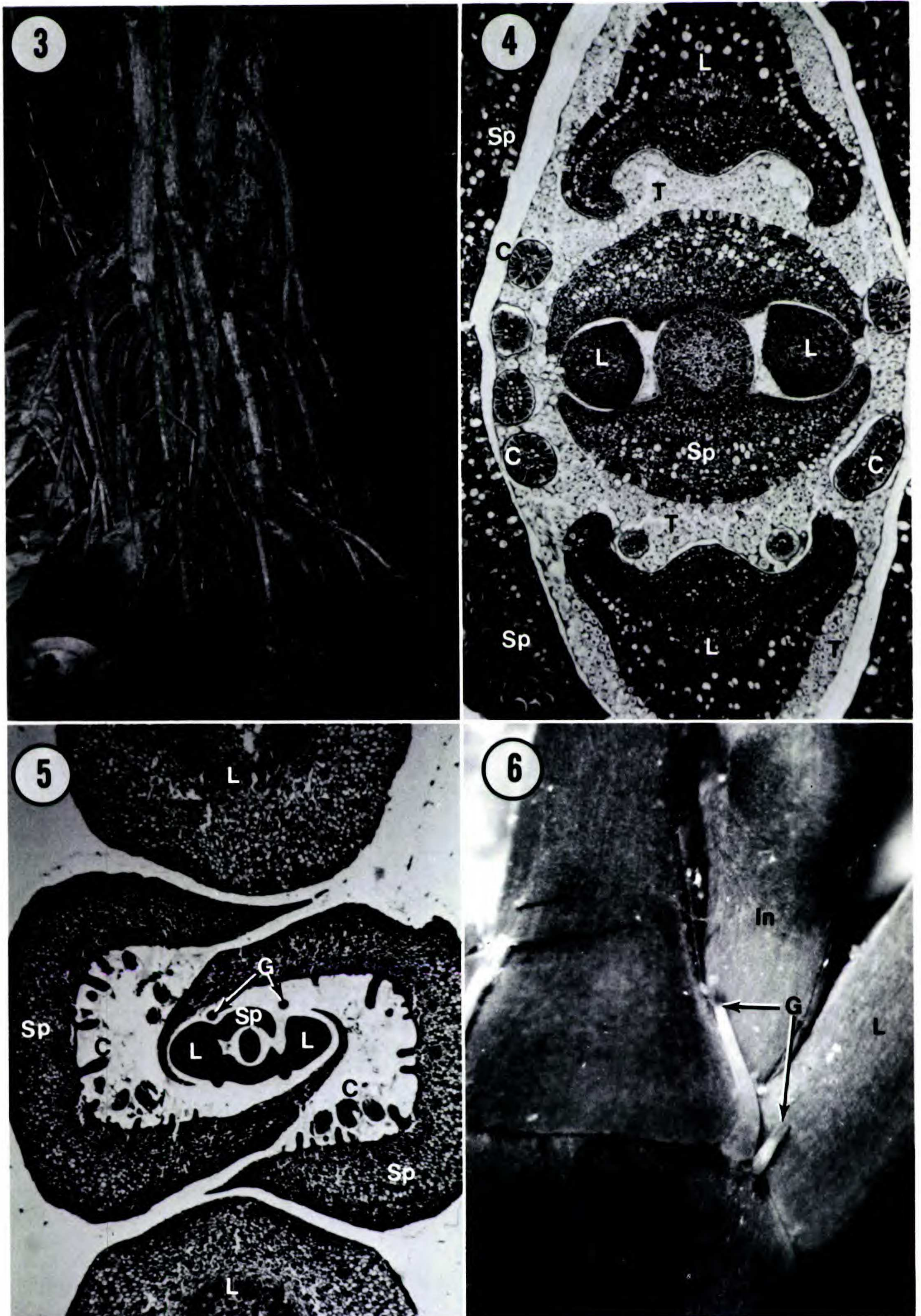
AERIAL ROOTS

Members of at least seven genera of Rhizophoraceae characteristically form aerial stilt roots, which have been described in greatest detail for the mangrove taxa (Troll, 1943). The genus *Rhizophora* (“root-bearer”) is justly famous for its

remarkable stilt roots (Fig. 1), the development, anatomy, and function of which were not understood until recently (Gill & Tomlinson, 1971, 1977; Scholander et al., 1955). *Ceriops tagal* and species of *Bruguiera* also form stilt roots on the hypocotyl and base of the trunk, which coalesce to form the fluted, conical trunk base that is seen in older plants (Fig. 2).

Among the inland genera, *Gynotroches* and *Crossostylis* (Gynotrocheae) normally form thick stilt roots on the lower trunk; *Crossostylis grandiflora* is known as “palétuvier de montagne” in New Caledonia for this reason (Fig. 3). At least one species of *Carallia*, *C. brachiata*, forms abundant stilt roots in peat swamps (Ding Hou, 1958). Thus, prominent aerial roots occur in three of the four genera of Gynotrocheae, the inland tribe that is probably most closely related to the mangroves. Although aerial roots in Rhizophoraceae may be formed more abundantly in swamps (e.g., in *Gynotroches*), they are not limited to plants found in that habitat; *Crossostylis grandiflora* is characteristically found in hilly sites. It may well be the humidity of the air rather than the inundation of the soil that is a factor in the development of aerial roots in inland taxa.

Another root character that is not often considered in systematic analyses is the presence of root hairs. These are formed on roots of *Cassipourea* seedlings but are not found in any of the members of the Gynotrocheae or Rhizophoreae that we have studied. Absence of root hairs from Rhizophoreae



FIGURES 3-6. *Stilt roots and vegetative bud morphology of inland Rhizophoraceae.*—3. *Stilt roots of Crossostylis grandiflora, one of at least three inland genera in which they occur (New Caledonia).*—4. *Transverse section of branch tip of Cassipourea elliptica, showing decussate phyllotaxy and valvate stipules.*—5. *Transverse*

may have a simple functional explanation if, as suggested by Tomlinson (1986), the endodermis is the site of the salt excluding mechanism, rendering an elaborated root surface unnecessary. Consequently, the root surface instead is elaborated by production of capillary rootlets (Attims & Cremer, 1967). This does not account for the absence of root hairs from Gynotrocheae, however.

Only one genus of Anisophylleaceae is known to possess any kind of aerial roots. *Combretocarpus* sometimes produces unique, diminutive (1–4 cm), negatively geotropic aerial roots on the trunk, usually 1–2 m above the soil (or water) level. However singular these may be, they bear no resemblance to the stilt roots of Rhizophoraceae, neither in development nor in mature anatomy and morphology, and cannot be considered a synapomorphy between the two families.

WOOD ANATOMY

A more detailed consideration of the wood anatomy of Rhizophoraceae and Anisophylleaceae appears elsewhere (Keating & Randrianasolo, this volume), but several specific points merit brief mention here. Indisputably, wood anatomical character states are very variable within Rhizophoraceae (Marco, 1935; van Vliet, 1976); however, we deem it poor systematic practice to use this variability as license to draw a relationship between the woods of these two families without any consideration of adaptive significance of wood structure. A number of significant differences could be discussed, but we wish to cite only a few. All Anisophylleaceae have alternate intervessel pitting with coalescent apertures, which are not found in any Rhizophoraceae. A limited amount of alternate pitting occurs in some species of *Carallia*, clearly as a specialization that has arisen within that genus and is thus not relevant to interfamilial relationships. The narrow vessels and scalariform perforation plates of Rhizophoraceae are distinctive and related to the low negative pressures induced by the saline environment, as discussed in Tomlinson (1986).

At the request of P. Baas, E. Wheeler (pers. comm.) compared wood anatomical characteristics of Anisophylleaceae with those of the Gynotrocheae and her computerized data base of 5,000 species. Although the character set was not specified and

clearly did not include coalescent apertures, absent from Rhizophoraceae (van Vliet, 1976), the coded characters of woods of Anisophylleaceae match those of at least some species of *Carallia* and, to a lesser extent, *Gynotroches* and *Crossostylis*. Significantly, woods of Anisophylleaceae are similar neither to those of the mangrove genera nor, more importantly, to those of any Macariseae. Therefore, if the wood anatomical similarities between Anisophylleaceae and *Carallia* were taken as synapomorphies, it would then be necessary to include the Anisophylleaceae as a subtribe of Gynotrocheae (see Fig. 27), which in turn requires us to hypothesize parallel reversals in at least 20 (probably closer to 50) vegetative, chemical, embryological, floral, fruit, seed, embryo, and seedling characters (see Table 1 and Dahlgren, this volume). As this is both extremely unparsimonious and biologically completely implausible, we conclude that the similarities in wood anatomy represent homoplasies and are not systematically significant in this case.

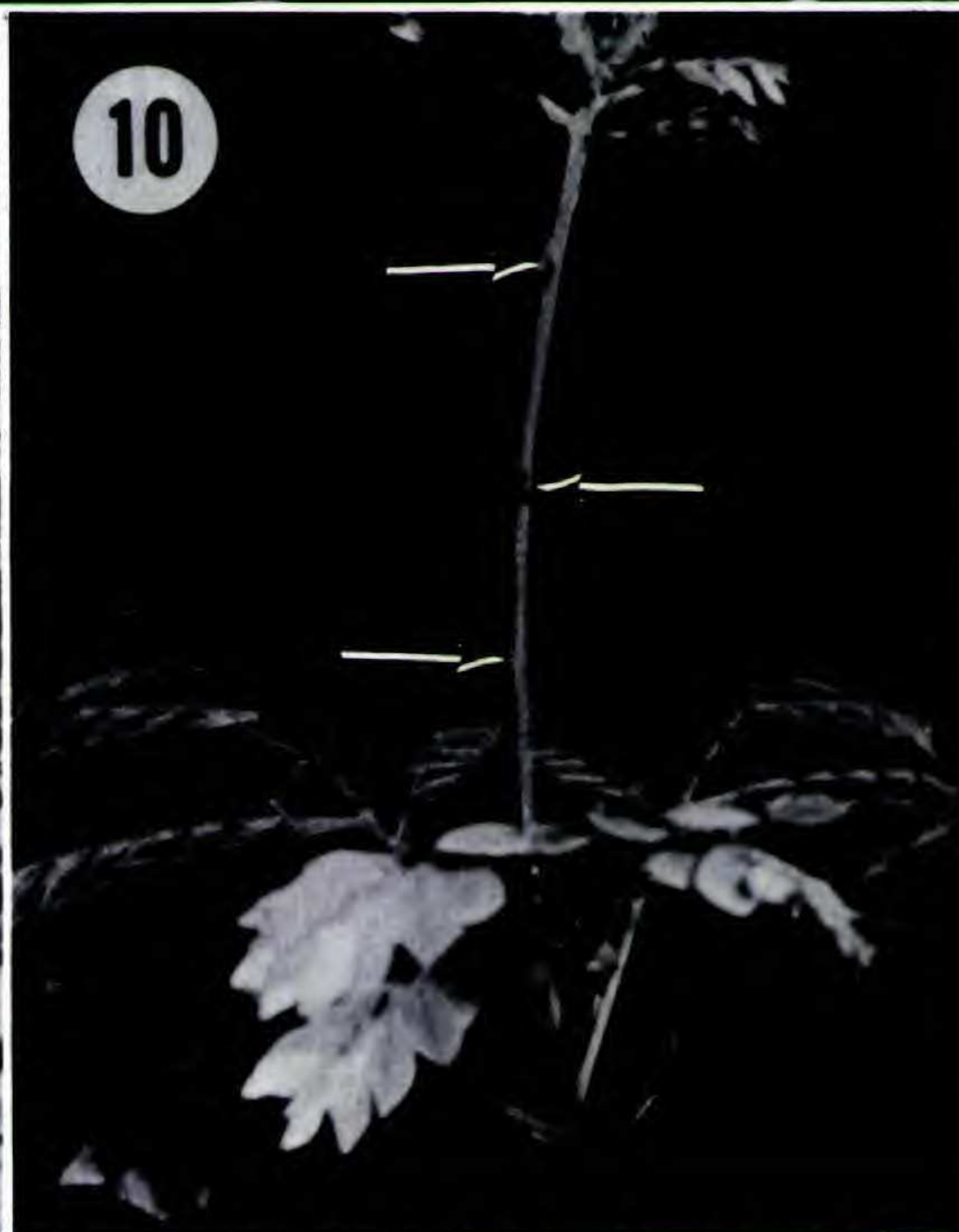
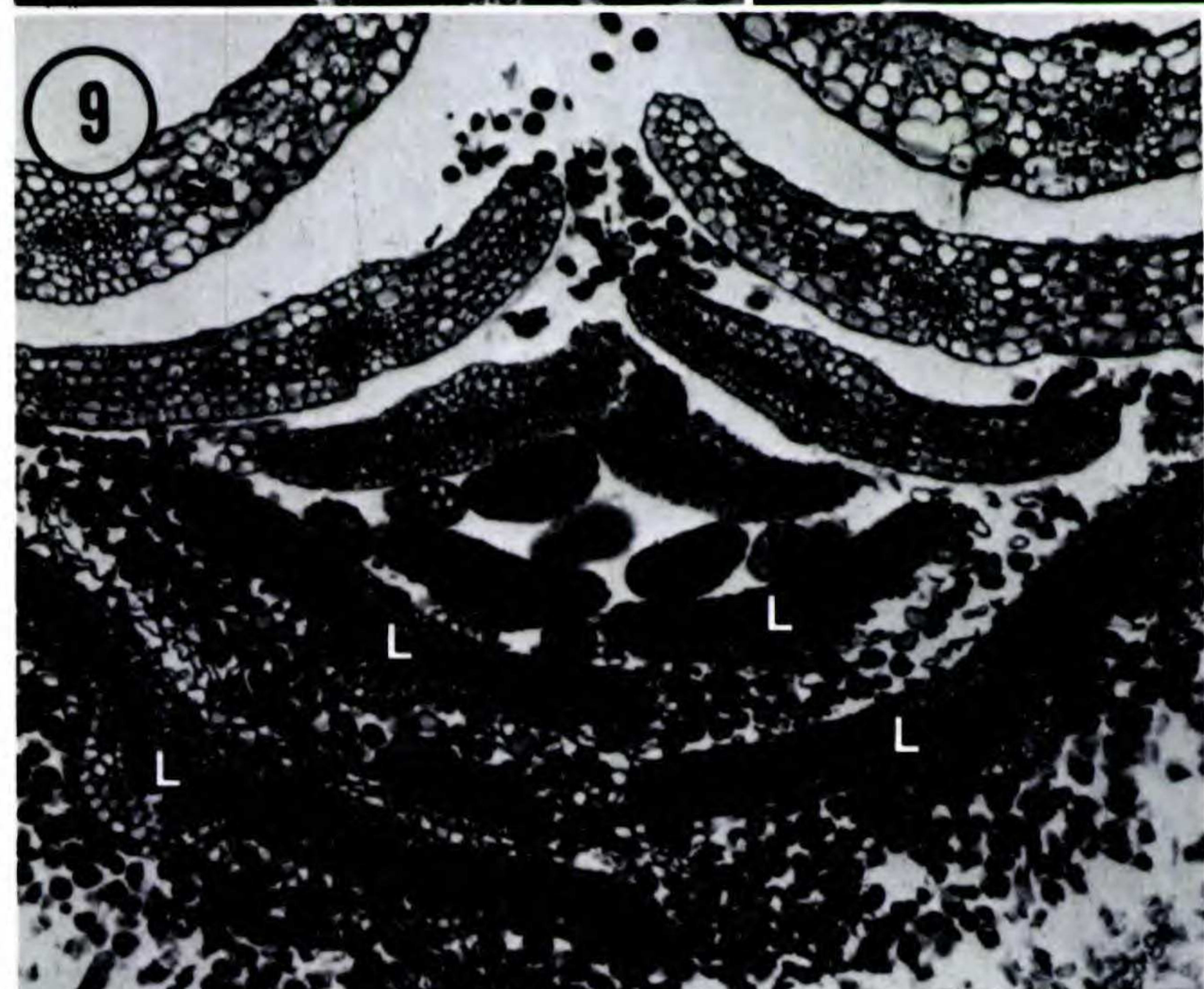
PHYLLOTAXY AND NODAL ANATOMY

Phyllotaxis is the one systematic difference between Rhizophoraceae and Anisophylleaceae that seems to be widely known: Rhizophoraceae have opposite leaves with interpetiolar stipules, whereas most Anisophylleaceae have alternate, exstipulate leaves. Certain additional details may ultimately prove helpful in understanding infrafamilial systematics.

In all Rhizophoraceae, the interpetiolar stipules bear colleters that secrete gummy substances onto the buds. In *Rhizophora stylosa*, this secretion contains galactose (Primack & Tomlinson, 1978), but whether its primary function is to deter herbivory (either through direct toxicity to insects or by attracting insectivorous birds) or merely to lubricate the expanding leaves while protecting them from desiccation is uncertain.

There are tribal distinctions in bud morphology within Rhizophoraceae. In *Cassipourea*, the stipules are valvate and pubescent (in addition to bearing colleters), and the leaves are truly decussate, that is, successive pairs of leaf primordia are initiated at exact right angles to one another (Fig. 4). Some reorientation of the leaves may occur during and after expansion. However, the usual descrip-

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section of branch tip of *Carallia borneensis*, showing imbricate stipules and bijugate phyllotaxy (successive pairs of primordia not perpendicular).—6. Extrastipular glands of *Carallia borneensis*. C, colleter; G, gland; L, leaf primordium; Sp, stipule; T, unicellular trichomes.



tion of phyllotaxis in all Rhizophoraceae as decussate holds only for the tribe Macarisieae and for *Pellacalyx* (Gynotrocheae). Tomlinson & Wheat (1979) showed that phyllotaxis in all genera of Rhizophoraceae is actually bijugate, with successive leaf pairs offset by angles of 70°–80°. Except for *Pellacalyx*, which has many autapomorphic features, all genera of Gynotrocheae also have bijugate phyllotaxy (Fig. 5). At least several species of *Carallia* bear extrastipular glands in addition to the colleters (Fig. 6). Interestingly, all genera with bijugate phyllotaxy have imbricate stipules, whereas those with decussate leaves have valvate stipules.

As discussed in greater detail later, overall tree architecture in Rhizophoraceae is variable, to some extent in relation to habitat differences. However, the basic architectural character of systematic interest is that the trunk and branches are only minimally or not at all differentiated; plagiotropic axes may be lacking altogether.

Anisophylleaceae are universally characterized as having alternate, exstipulate leaves, but at least one species of *Anisophyllea*, *A. disticha*, has structures interpretable either as minute stipules or large glands (Figs. 8, 11). The phyllotaxy of plagiotropic branches of this genus is unique among angiosperms: there are four orthostichies of leaves, two of reduced leaves on the upper side, and two of full-sized leaves along the lower side (Figs. 7–9). Orthotropic axes, in contrast, bear helically arranged reduced leaves in a conventional 2/5 helix (Figs. 10–12; Vincent & Tomlinson, 1983); thus, differentiation of axes is pronounced, at least in this genus.

Based primarily on study of herbarium material, Ding Hou (1958) stated that anisophylly of this kind is characteristic of only two species of *Anisophyllea*. However, our fieldwork shows that anisophylly is also the rule in plagiotropic axes of at least *A. cinnamomoides*, *A. ferruginea*, *A. griffithii*, and *A.*, sp. nov. Ding Hou (1958), but that the reduced leaves in these species are sometimes very small and caducous and hence are rarely seen

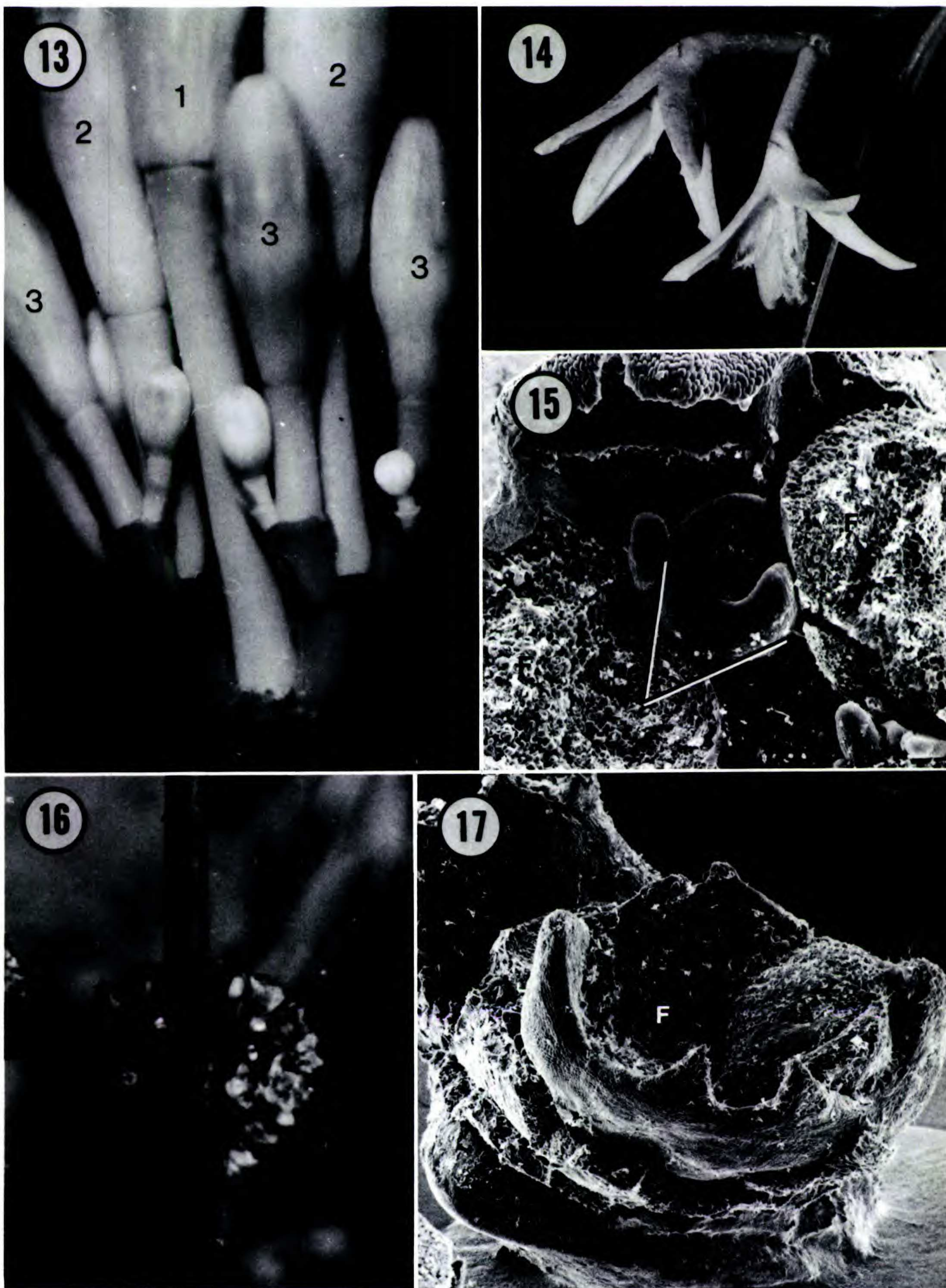
in herbarium specimens. (Their scars, ordinarily lacking axillary buds, can often be detected.) It thus seems likely that both anisophylly and the unique tetrastichous phyllotaxy are uniform for Asian species of the genus. *Anisophyllea cinnamomoides*, which forms a moderate-sized tree, has the same architecture as a sapling that has been described in detail for adult *A. disticha* (Vincent & Tomlinson, 1983). Consequently, one may interpret the latter species as a permanently juvenile form. Herbarium study of virtually all other described species of the genus revealed that anisophylly occurs in all but a group of two or three closely related species (Juncosa, pers. obs.), a conclusion corroborated by the field studies of Floret (pers. comm.). He additionally communicated that in at least one rhizomatous shrubby species of a habitat subject to both severe seasonal drought and periodic fires, axis differentiation is seasonal rather than architectural.

Our knowledge of phyllotaxy and architecture in other genera of Anisophylleaceae is even poorer than in *Anisophyllea*; no reference mentions anisophylly in the other three genera. It does occur in *Poga* and *Polygonanthus*, although the strict alternation of leaf types seen in *Anisophyllea* is not preserved in all parts of the axes of *Polygonanthus*: several small leaves occur in succession at the bases of some branches, but these reduced leaves may be lacking distally (Juncosa, pers. obs.).

A more detailed discussion of leaf anatomy appears elsewhere in this volume, but a few characters bear mention here. It is not generally understood that in most inland Rhizophoraceae, juvenile and usually also the adult leaves are variously toothed or crenate, not entire as is usually stated. Only in Rhizophoraceae are the leaves consistently entire, one of many characters in which derived states (within the family) are exhibited by the specialized mangrove genera. Other leaf characteristics of this tribe, such as the succulent hypodermal layer, terminal tracheids, and frequently abundant sclereids, are probably all adaptations to the mangrove hab-

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FIGURES 7–12. *Habit and development of axes of Anisophyllea disticha*.—7. *Plagiotropic branch of large-leaved Sarawak variety of A. disticha*. Both ranks of scale leaves (arrows) are on upper side of branch.—8. SEM of apex of plagiotropic branch. Nonvascularized “glands” are of uncertain homology, although they do occur in stipular sites. (Micrograph courtesy of Nancy Dengler.)—9. Transverse section of plagiotropic branch tip at level of shoot apex. Scales leaves (Sc) have rather empty (vacuolate) cells; foliage leaves (L) have densely staining (meristematic) mesophyll.—10. Top of plant of *A. disticha* (photographed in Brunei), showing pseudowhorls of plagiotropic branches and orthotropic axis bearing only scale leaves (arrows).—11. SEM of apex of orthotropic axis. All leaf primordia are of scale leaves. “Glands” are very evident at stipular sites. (Micrograph courtesy of Nancy Dengler.)—12. Transverse section of orthotropic axis at level of shoot apex; leaves are arranged in a normal phyllotactic spiral.



FIGURES 13–17. Inflorescence morphology of Rhizophoraceae.—13. Open-branched cymose inflorescence of *Bruguiera parviflora* (Malaysia). Order of maturation of flowers is indicated by numbers. First branching event is dichasial, others generally monochasial.—14. Bifurcate inflorescence of *Rhizophora mangle* (Florida). In other species, up to 32 flowers occur in evenly bifurcating inflorescences.—15. SEM of developing inflorescence of *R. mangle*, showing aborted bracteole and terminal floral apex (bracket) between the sites where maturing flowers were removed (F).—16. Fasciculate inflorescence of *Gynotroches* sp. (Sarawak).—17. SEM of ultimate inflorescence branch of *Pellacalyx cristatus*. Opposite bractlets are fused into a toothed cup; terminal flower has been removed (site marked F). Axillary branch (A) is enclosed by fused prophyllar bractlets.

itat. An achlorophyllous hypodermal layer is also found in at least three genera of Gynotrocheae, but not in *Cassipourea* (Macarisieae), so that character may be of phylogenetic significance as well.

Nodal anatomy also seems to distinguish the two families, as the Rhizophoraceae are characterized by multilacunar nodes with split-lateral traces (Howard, 1970, 1979), whereas Anisophylleaceae have unilacunar nodes (*Anisophyllea*: Geh & Keng, 1974; Vincent & Tomlinson, 1983; *Combretocarpus*: Juncosa, unpubl. obs.).

INFLORESCENCE

The inflorescence in Rhizophoraceae is fundamentally cymose, both in open-branched and fasciculate forms. Flowers of large-flowered species of *Bruguiera* are solitary, presumably by reduction. The first branching event is dichasial (sometimes trichasial in *Ceriops* and in *Carallia brachiata*); subsequently, branching is usually monochasial (Fig. 13). In *Rhizophora*, *Kandelia*, and *Crossostylis*, inflorescences bifurcate throughout (Fig. 14), but the division appears to be pseudodichotomous. Although the apices terminating the sympodial units do not develop into flowers in these genera, their vestiges can often be found (Fig. 15). Interestingly, both open-branching and fasciculate forms (in which the branch internodes do not elongate; Fig. 16) are found in all three tribes. It therefore appears that condensation of the inflorescence evolved in parallel three times. A single bract subtends each branch, thus there is a pair of bracts at each node, even when further development of one of the two branches is suppressed in the monochasial portions of the inflorescence. Pairs of bracteoles also subtend each flower. The bracteoles bear colleters similar in distribution, development, and mature anatomy to those of the stipules and secrete a sticky, rubbery coating over the floral primordia. In *Pellacalyx*, the pairs of bracts are fused into a toothed cup-shaped structure superficially resembling an epicalyx, but subtending minute axillary buds in addition to the terminal flower (Fig. 17).

Inflorescences in the Anisophylleaceae are paniculate or racemose and usually somewhat open-branched. A single bract subtends each branch and flower. In *Anisophyllea disticha*, male and female flowers occur in separate inflorescences, but in most other species and genera in the family, the two floral types are mixed in all inflorescences. Thus, although the differences are to some extent an extension of the phyllotactic differences of the vegetative shoots, there is no inflorescence character

state common to both Rhizophoraceae and Anisophylleaceae.

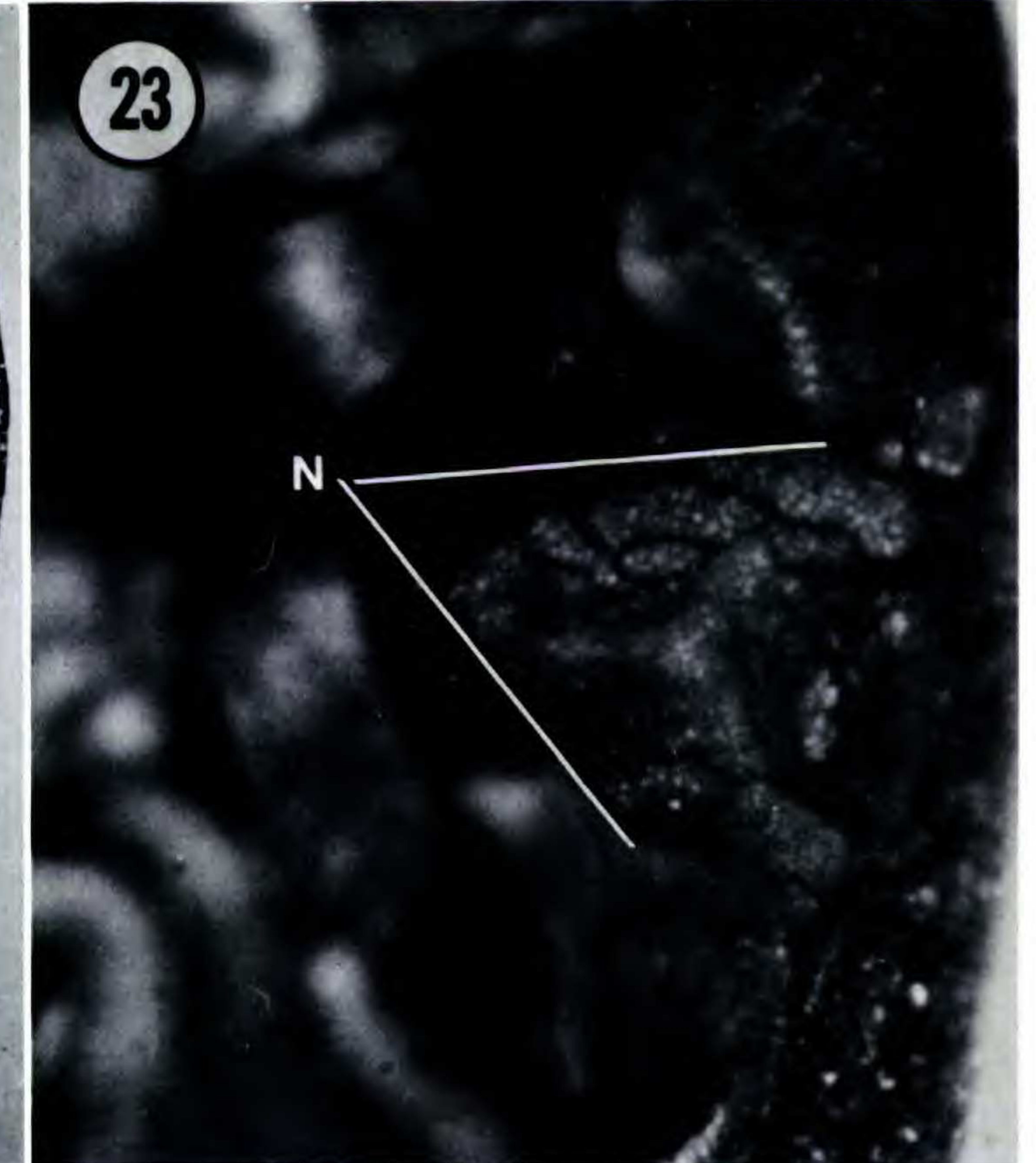
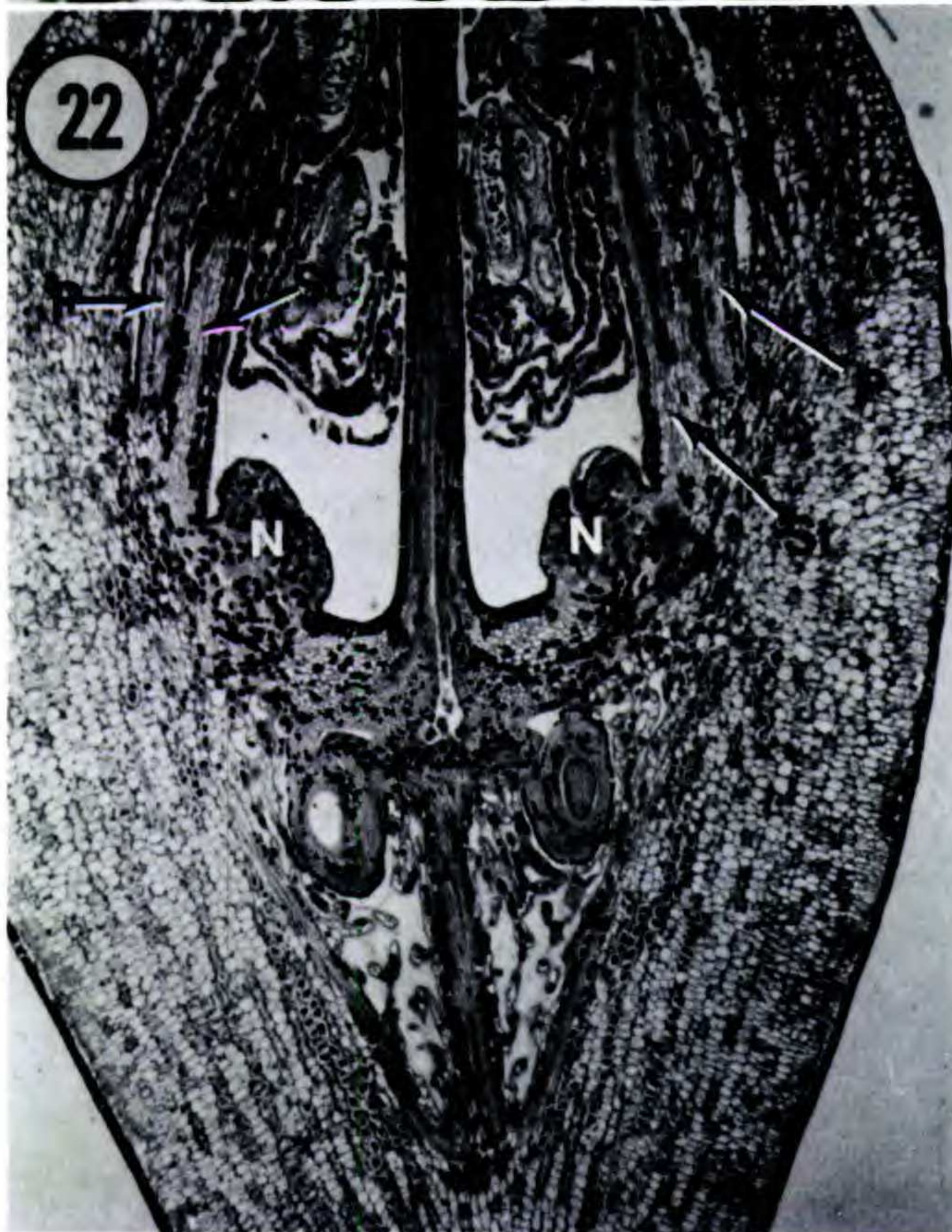
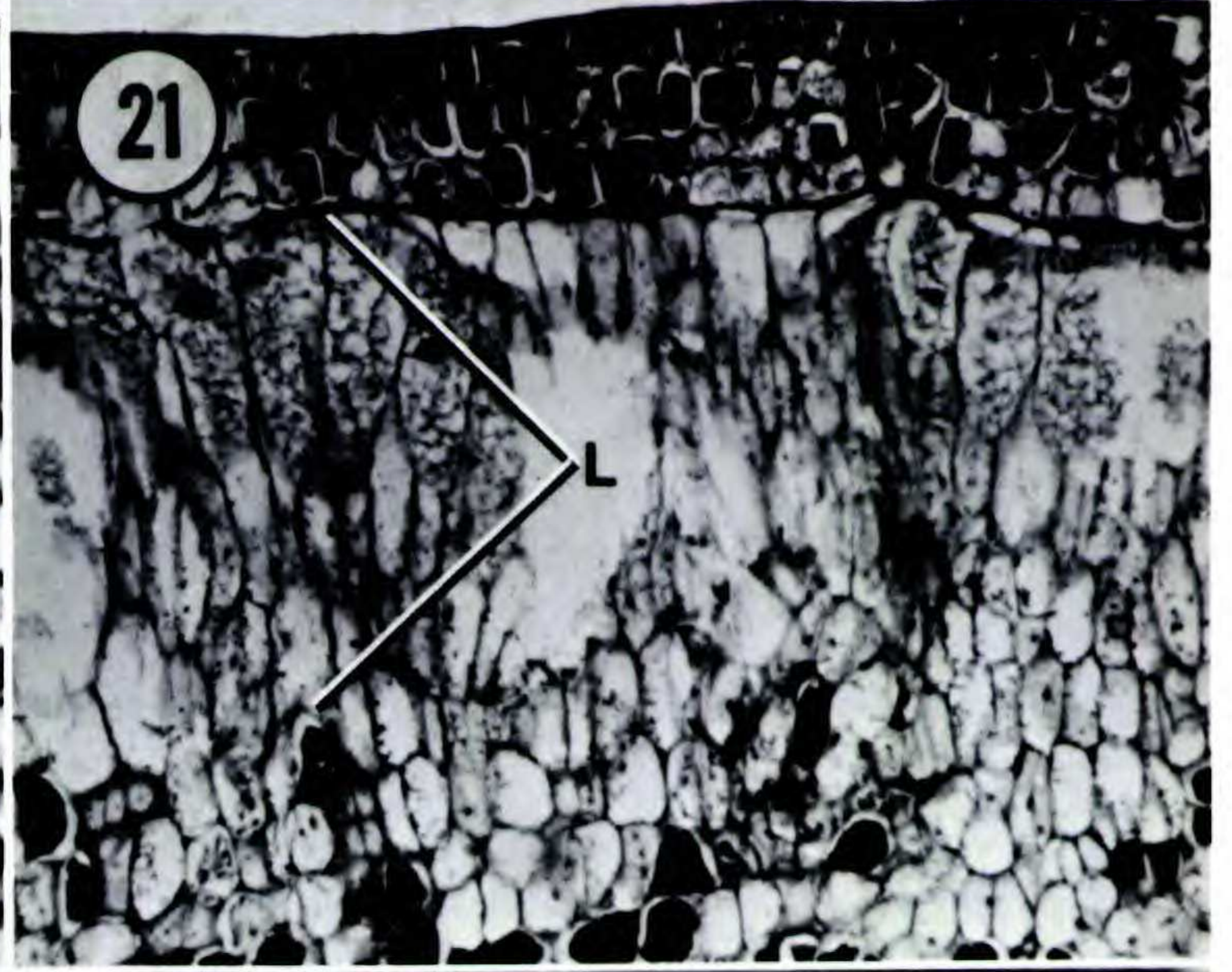
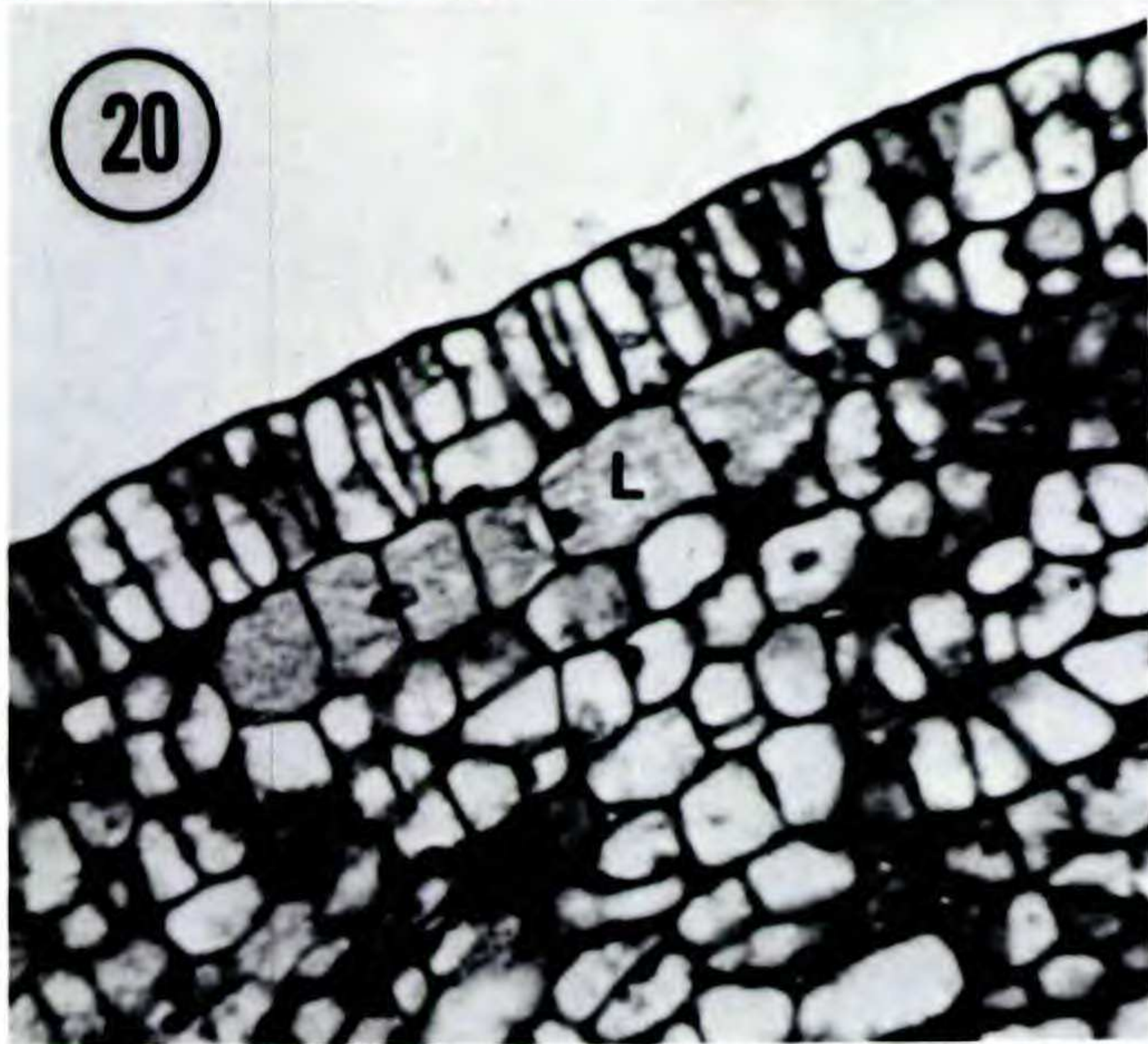
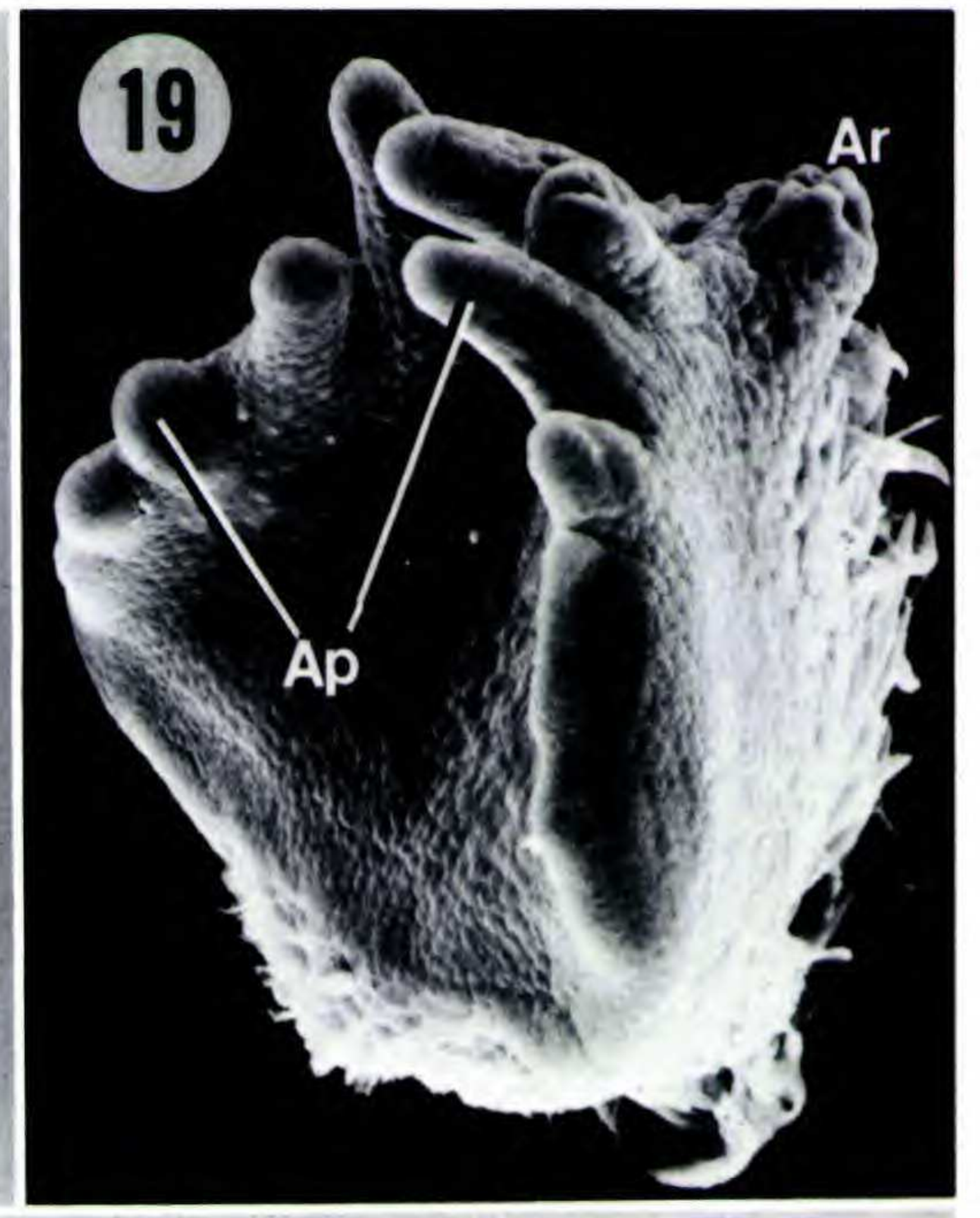
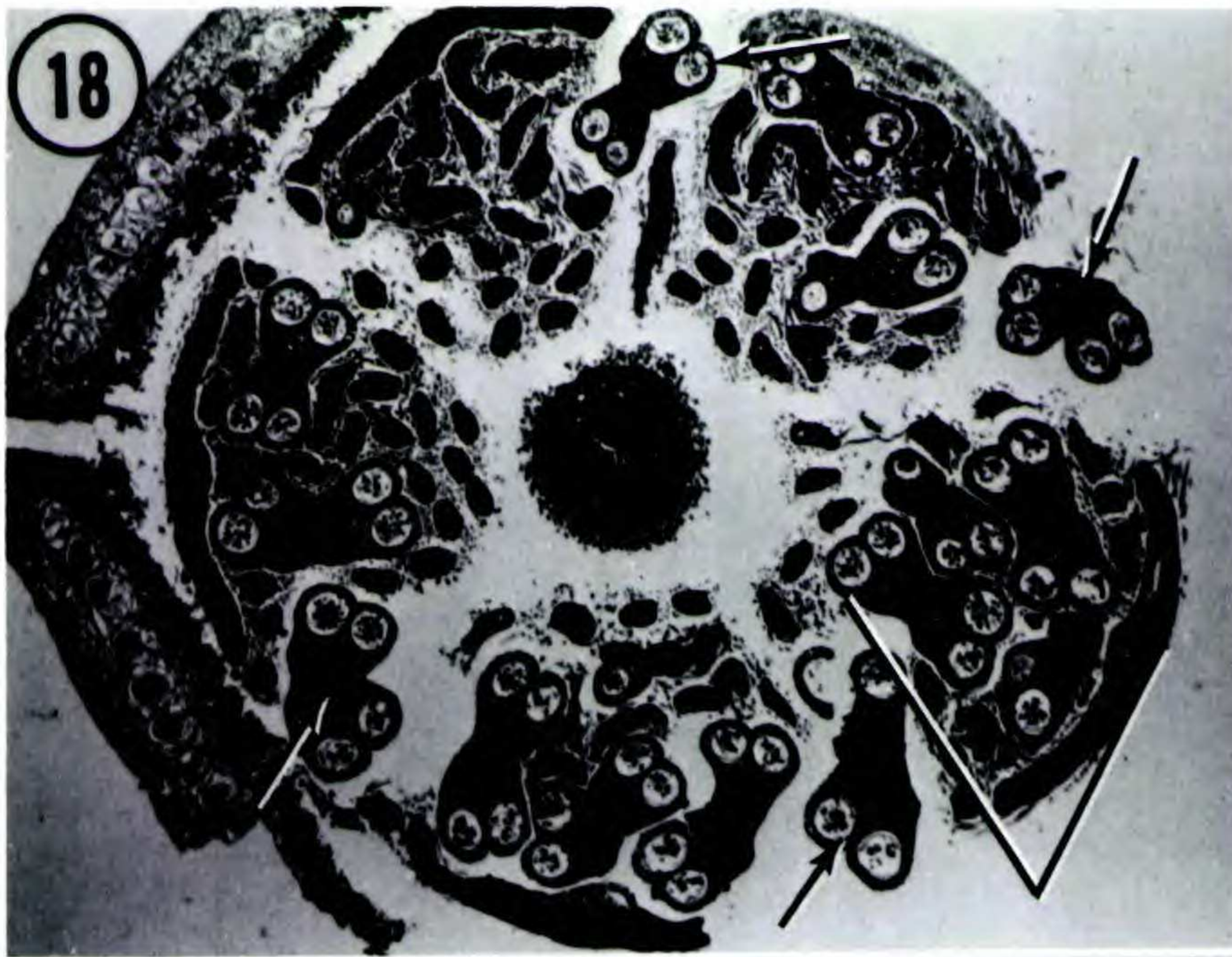
FLORAL MORPHOLOGY AND DEVELOPMENT

In most Rhizophoraceae the flowers are bisexual, but exceptions are found in both inland tribes. *Gynotroches* (Gynotrocheae) is dioecious; in male flowers, the ovary and ovules develop and at least the early stages of megagametogenesis occur, but the style atrophies distally instead of elongating. In female flowers, anthers and sporogenous tissue develop, but normal microsporogenesis seems to be interrupted shortly after meiosis. At least some species of *Crossostylis* (Gynotrocheae) are polygamodioecious, with many individuals bearing only functionally female flowers (Smith, 1981). Among the Macarisieae, *Blepharistemma* and *Sterigmapetalum* are reported to be polygamodioecious and dioecious, respectively, but developmental details are lacking.

Although mature floral structures in Rhizophoraceae are remarkably diverse, especially in relation to contrasted pollination mechanisms (Juncosa & Tomlinson, 1987), early developmental stages are generally very similar. Floral characters that unify the family include petal development and mature morphology, the generally diplostemonous androecium, and the presence of laticifers.

These generalizations are based upon study of nine of the fourteen genera of the family, including all genera of tribes Gynotrocheae and Rhizophoreae and one of Macarisieae (*Cassipourea*). Inasmuch as the mature morphology of flowers of Macarisieae varies very little, especially in comparison with that of genera of the other two tribes, this survey may be taken as encompassing nearly all aspects of floral evolution in the family.

Petals in rhizophoraceous taxa are fundamentally bifid, with a prominent terminal arista, and they enclose groups of one or more stamens individually, rather than forming a whorl that collectively surrounds the androecium as a whole (Fig. 18). This distinctive petal veneration is to our knowledge found in only one other family of dicotyledons, Rhamnaceae. Usually, several to many filamentous appendages develop on the distal margins of the two main lobes of the petal (Fig. 19). Mature petals of *Crossostylis* appear to lack appendages, but this results from the suppression of development of appendages that are initiated in exactly the same mode and position as in other genera. This may also be the case in *Anopyxis*, which is described as having entire petals. Only in *Rhizophora*, the most specialized genus in the family, are the marginal petal appendages truly absent, even though



petals still bear a terminal arista and enclose individual stamens. Although fringed petals are found in a number of other families, including Anisophylleaceae, their mature morphology and probably also early development do not resemble those of petals of Rhizophoraceae.

Another distinctive characteristic of rhizophoraceous flowers is the presence of a layer of laticiferous cells in the ovary and calyx. These cells may form a more or less continuous layer (*Cassipourea* and Rhizophoraceae; Fig. 20) or may grow radially, usually dividing periclinally (*Crossostylis* and *Carallia*; Fig. 21). In *Gynotroches* and *Pellacalyx*, the laticifers are further modified into disconnected canals or idioblastic cells. In most genera, the epidermis surrounding the laticiferous layer divides periclinally, becoming 5–7-seriate.

The androecium in most Rhizophoraceae is diplostemonous, and the antisepalous whorl of stamens is ordinarily initiated earlier than the antipetalous whorl. Nearly all Macarisieae and at least one genus in each of the other two tribes exhibit this basic floral pattern, which we believe to be ancestral for the family. However, significant modifications have arisen in parallel in all three tribes. For example, in *Carallia* and *Pellacalyx* (Gynotrocheae), the antipetalous stamens are initiated earlier than the antisepalous stamens (Juncosa, in press). Also, one genus in each of the three tribes has polyandrous flowers, probably a homoplasy (see Fig. 27). This indirect conclusion, based upon the likely cladistic relationship of the genera, is also supported by the diversity of developmental pathways that give rise to the numerous stamens in these three genera. In *Kandelia*, the polyandrous mangrove genus, the supernumerary stamens result from the initiation of about five stamens on a large common primordium that also produces a petal (Juncosa & Tomlinson, 1987). In the distantly related inland genus *Cassipourea* (Macarisieae), additional stamens are not initiated together with the petals, but the vas-

culature of each petal is closely associated with that of several nearby stamens. In several species of *Crossostylis*, the groups of stamens are found opposite the sepals instead of the petals (Smith, 1981).

All Rhizophoraceae have a single style and stigma, although in *Gynotroches* the stigmatic lobes may be rather long. The separate stigmatic lobes may be discernable at gynoecial initiation (e.g., *Gynotroches*, *Pellacalyx*), or the gynoecium may arise as a single toroidal primordium (e.g., *Carallia*, *Bruguiera*). Most Macarisieae have fully superior ovaries, but two genera of this tribe and most other genera in the family have half-inferior or completely inferior ovaries. Details of the development and vasculature of the ovary appear in Juncosa (in press). The occurrence of a superior ovary in female flowers of *Gynotroches* is probably a reversion from the half-inferior condition, which occurs in the functionally male flowers of the same genus. (As detailed above, unisexuality occurs in this genus by very late-developmental changes; the basic morphology of the two kinds of flowers is quite similar.) Additional support for this hypothesis comes from the diversity of placentation types in *Gynotroches* (Ding Hou, 1958); placentation in all other genera of Rhizophoraceae is invariably apical-axile.

Rhizophoraceae typically have 3–5 carpels (whether the locules are completely separate or not) and only two ovules per carpel, but an increase in the total number of ovules and seeds has evolved in several ways. In *Crossostylis*, this is achieved by multiplication in the number of carpels, up to as many as 20. In *Gynotroches* there are only five carpels, but each contains up to eight ovules. In *Pellacalyx* both the number of carpels and the number of ovules in each is increased.

The presence of a floral disc is often used as a systematic character, but an imprecise understanding of the initiation and development of this organ

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FIGURES 18–23. *Floral morphology and anatomy of Rhizophoraceae and Anisophyllea*.—18. *Transverse section of flower bud of Cassipourea elliptica*; a petal, largely represented by its filamentous appendages, and the small group of stamens that it encloses are indicated by a bracket. Note that antisepalous stamens are not enclosed by petals but stand between their lateral abaxial sides (arrows).—19. *SEM of petal of Pellacalyx cristatus at an early developmental stage, showing filamentous appendages (Ap) and terminal arista (Ar)*.—20. *Continuous uniseriate laticifer of Bruguiera exaristata at an early stage of development. Periclinal divisions are beginning in the epidermis, which will become 5–7-seriate, but laticifer cells seem only to expand somewhat periclinally, not to divide*.—21. *Longitudinal section of flower of Crossostylis biflora, showing anticlinally expanded laticiferous cells (L); these seem also to divide periclinally, but this is difficult to establish*.—22. *Medial longitudinal section of flower of Carallia borneensis, showing that the putative nectary (N) is strictly intrastaminal. St, stamen; P, petal*.—23. *Epi-illumination light micrograph of crenate nectary (N) of Anisophyllea obtusifolia. Divisions extend to the base of the nectary. (Material courtesy of Hiroshi Tobe.)*

may have led to considerable confusion and misinterpretation in the study of angiosperm phylogeny. In Rhizophoraceae, a nectarial ring arises inside the androecium late in floral development (Juncosa & Tomlinson, 1987). Thus, the stamens are not inserted on this ring, nor is it part of the androecium (Fig. 22). This important distinction is clearly illustrated by the genus *Bruguiera*, in which the androecium is initiated as a toroidal primordium, upon which separate stamen primordia later develop. Later, a separate toroidal primordium is initiated internally (centripetally) to the androecium and ultimately develops into the nectary. Some significant modifications to this basic pattern occur in certain inland genera in tribe Gynotrocheae, but the oft-cited character state "stamens inserted on a disc" is certainly incorrect for nearly all Rhizophoraceae.

Unfortunately, detailed information on development of flowers of Anisophylleaceae is not available, but descriptions of their mature morphology (Ding Hou, 1958; Tobe & Raven, 1987b) reveal several major differences from Rhizophoraceae. Petals of several genera of Anisophylleaceae are fringed (*Poga*, *Anisophyllea*) or weakly divided (*Combretocarpus*), but the distinctive morphology described above for Rhizophoraceae does not occur here. In particular, the prominent terminal arista is absent, and even in the few cases where the petals are bifid (some species of *Anisophyllea*), they do not individually enclose one or more stamens. Other floral differences are seen in gynoecial morphology. The several styles are separate all the way to their bases in all Anisophylleaceae. The inferior ovary is evidently ancestral for the family (not superior, as in Rhizophoraceae). The morphology of the nectary in Anisophylleaceae is unusual. The mature nectary is both inter- and intrastaminal and is cleft to its base in many places (Fig. 23). Information on its development is lacking, but it is safe to speculate that it is likely to be very different from that of nectaries of Rhizophoraceae.

FRUIT AND SEED

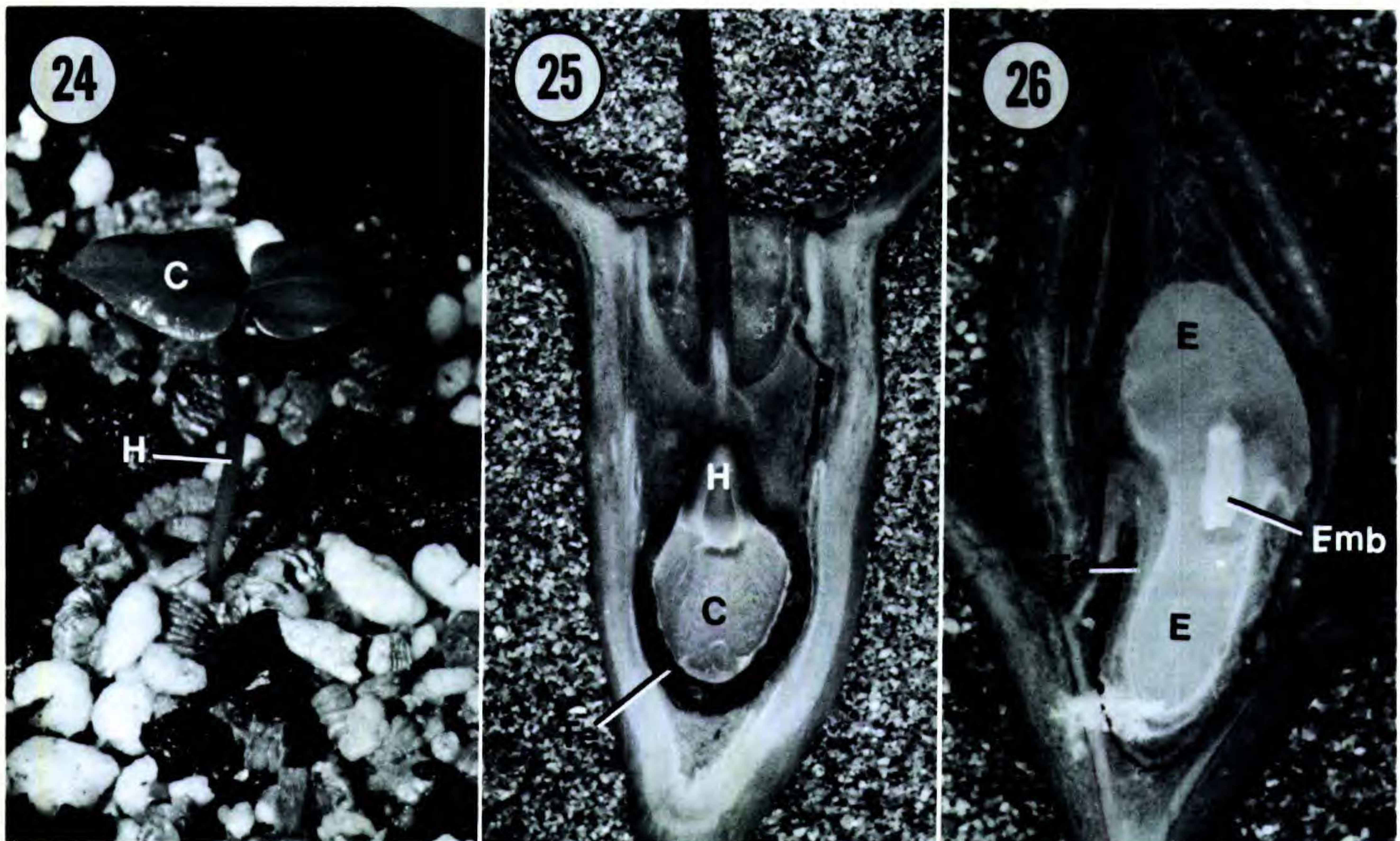
Within the Rhizophoraceae, a clear evolutionary trend can be seen in fruit structure. All Macarisieae have capsular fruits, although these vary in their degree of sclerification and in how readily they dehisce. The tough-fleshy capsules of *Cassipourea elliptica* (Sw.) Poir., for example, often (always?) drop from the trees unopened, dehiscing on the ground as they dry slightly; the arillate seeds are then carried off in great numbers by leaf-cutter

ants. Field observation on the Osa Peninsula of Costa Rica revealed that the ants carry the seeds into the nest, remove the arils, and discard the stripped seeds (Juncosa, pers. obs.). This may seem an unadaptive destination, but Prance (pers. comm.) correctly pointed out that the dispersal function is satisfied by those seeds dropped along the way by accident or as a result of such common disturbances as rain showers. In *Cassipourea*, presence of the aril does not inhibit germination. The comparatively large (3.5 cm), woody capsules of *Anopyxis* have been described as indehiscent, but we imagine that the description was based on immature fruits; it seems overwhelmingly likely that a canopy tree with winged seeds would also have dehiscent fruits. Consideration of the probable cladistic relationship of genera yields the interesting conclusion that some or all of the arillate-seeded genera were derived from winged-seeded ancestors. The homology of wing and aril is established by Tobe & Raven (this volume) on the basis of comparative morphology of mature seeds; these authors consider the aril to represent the ancestral condition, primarily because of its strong correlation with a superior ovary. Fruits of *Crossostylis* (Gynotrocheae) are also capsular, often only partly dehiscent, the small seeds falling out through the slots.

Fruits of all Gynotrocheae other than *Crossostylis* and those of all Rhizophoreae are baccate, and the seeds are naked. In *Gynotroches* and *Pellacalyx*, the many small seeds are embedded in a nearly homogeneous juicy berry. In *Carallia* and in Rhizophoreae, a distinctive loose spongy region develops below the ovules, allowing for the rapid early expansion of the seed(s). In *Ceriops*, *Kandelia*, and *Rhizophora* the superior portion of the ovary develops greatly in fruit.

The seed coats of all Macarisieae and most Gynotrocheae are characterized by a sclerified exotegmen (Corner, 1976; Juncosa, 1984a and unpubl.; Tobe & Raven, 1987b), but this structure is absent from seeds of *Carallia* and the Rhizophoreae. That this absence probably represents an evolutionary loss is supported by developmental evidence: the outer epidermis of the inner integument of *Carallia* ovules is histologically distinctive, as in other inland genera, but the cells fail to expand and sclerify.

Fruits of most Anisophylleaceae are drupaceous, unlike those of any Rhizophoraceae. The fruit of *Combretocarpus* is light and three-winged, so it is not surprising that the development of a heavily sclerified endocarp is suppressed. The seed coats of Anisophylleaceae lack a sclerified exotegmen and differ in other respects from those of Rhizo-



FIGURES 24–26. Seedling germination in Rhizophoraceae.—24. Epigeal germination in *Cassipourea elliptica*.—25. Viviparous germination by growth of hypocotyl in *Bruguiera exaristata*.—26. Viviparous germination by expansion of endosperm in *Rhizophora mangle*. C, cotyledon; E, endosperm; Emb, embryo; H, hypocotyl; Te, testa or seed coat.

phoraceae (Tobe & Raven, 1987a). Seeds of Anisophylleaceae also lack endosperm (Floret, 1979), which is present in all Rhizophoraceae.

EMBRYO AND GERMINATION

As far as is known, all inland Rhizophoraceae have epigeal germination and foliaceous cotyledons (Fig. 24) (*Cassipourea*: Juncosa, 1982a, b, 1984a; *Carallia*, *Pellacalyx*, and *Gynotroches*: Geh & Keng, 1974; Ng, 1980; Ng & Sanah, 1979; Ng, pers. comm.). Development of the embryo to a large seedling while still attached to the parent plant (vivipary) characterizes the Rhizophoreae and offers interesting material for comparative study. Germination morphology in these (mangrove) genera has been classified as “Durian-germination,” in which the hypocotyl elongates, but the cotyledons remain hidden (Ng, 1978). Both outgroup comparison (with all inland Rhizophoraceae) and comparative developmental morphology indicate that this is a modification of ancestral epigeal germination.

Among the Rhizophoreae, cotyledonary morphology varies. *Bruguiera* species have two or three cotyledons, which are thick and fleshy and remain permanently within the seed coat throughout the viviparous seedling development. The

development of these cotyledons and their median-plus-split-laterals vasculature reveals their foliaceous ancestry; they also subtend axillary buds (Juncosa, 1984b). In the more advanced Rhizophoreae, however, the cotyledons arise as a single toroidal primordium and form a solid cylindrical body, sometimes becoming 2–3-lobed distally; it is vascularized by many separate traces, evenly spaced. Vasculature of the cotyledonary body of *Kandelia* is intermediate between that of *Bruguiera* and that of *Ceriops* and *Rhizophora*.

In addition to being the only genus in the tribe with separate cotyledons, *Bruguiera* also exhibits the intermediate condition in the evolution of vivipary: the embryo grows to fill the seed completely, then germination occurs by elongation of the hypocotyl, much as in the nonviviparous inland genera (Fig. 25). Endosperm is not involved in viviparous germination. However, in *Ceriops*, *Kandelia* and *Rhizophora*, the micropyle is forced open by growth of the endosperm, which in *Rhizophora* may even carry the undifferentiated proembryo partially or entirely out of the seed (Fig. 26). In all genera, the cotyledonary body subsequently grows to fill the seed coat, with only a thin layer (usually one cell thick) of intervening endosperm. This persistent endosperm forms transfer cells (Juncosa, 1982a, b). A considerable amount

TABLE 1. Summary comparison of *Rhizophoraceae* and *Anisophylleaceae*. Refer to text for important details and exceptions.

	Rhizophoraceae (14 genera)	Anisophylleaceae (4 genera)
Growth	continuous	rhythmic
Branch differentiation	minimal	extreme
Wood	very heterogeneous	large vessels, alternate pitting with coalescent apertures
Aerial stilt roots	formed in <i>Gynotrocheae</i> and <i>Rhizophoreae</i>	not formed
Phyllotaxis	leaves opposite (bijugate or decussate)	leaves alternate (distichous or tetrastichous)
Stipules	present, interpetiolar	vestigial or absent
Leaf morphology	toothed margins in inland genera	entire margins
Nodal anatomy	tri- or multilacunar, split laterals	unilacunar
Inflorescences	cymose (dichasial changing to monochasial)	racemose (to paniculate)
Floral histology	subepidermal laticifers	no laticifers
Petals	bifid, fringed, with terminal aristata, convolute	sometimes fringed or divided, not folded
Ovary	superior to inferior	inferior
Fruit	capsular to baccate	drupaceous or winged
Seed coat	sclerified exotegmen in most inland genera	sclerified exotegmen absent
Seed	albuminous	exalbuminous
Cotyledons	laminar (modified in mangroves)	minute or absent
Germination	epigeal or viviparous	hypogeal
Sieve-tube plastids	Pv-type	S-type
Chromosome number	$n = 14, 18, 21, 32$	$n = 7, 8$

of endosperm emerges from the seed coat in all three genera. In *Rhizophora*, this endosperm merely forms a collar around the (intercalary) meristematic upper portion of the hypocotyl (Juncosa, 1982a), but in *Ceriops* and *Kandelia* it grows invasively into the ovary wall, forming an irregularly branched haustorium.

Embryo anatomy and germination in *Anisophylleaceae* differ sharply from that of any *Rhizophoraceae*. The embryo in *Anisophylleaceae* has a massive hypocotyl, with the cotyledons represented by minute scales (*Anisophyllea*) or even entirely absent, not even detectable under microscopic examination (Poga; Floret, 1979). Germination is hypogeal, with all of the morphological characteristics associated with that growth habit (e.g., earliest epicotyledonary leaves cataphylls, not foliaceous as in epigeal germination). In *Anisophyllea disticha*, shoots may arise from both ends of the seed (Geh & Keng, 1974). Regrettably, anatomical information is lacking.

CYTOLOGY

Chromosome numbers are often regarded as systematically important, but only a few genera of these two families have been counted. *Rhizopho-*

reae uniformly have $n = 18$ (Sidhu, 1968; Yoshio-ka et al., 1984). *Crossostylis* has $n = 14$ (Tobe & Raven, pers. comm.); *Anopyxis*, $n = 32$ (Mangenot & Mangenot, 1958). Counts of $n = 18$ and $n = 21$ have been reported in *Cassipourea* (Weiss, 1973; Juncosa, unpubl.); further data from this large genus are urgently needed. Chromosomes throughout *Rhizophoraceae* are extremely small, most of them being about $1 \mu\text{m}$ long.

Chromosome numbers in *Anisophylleaceae* have been counted only in sectioned material (Tobe & Raven, 1987a) but show quite different numbers ($n = 7, 8$), which have not yet been observed in *Rhizophoraceae*.

Other systematic characters that have recently proved revealing include sieve-tube plastids. Behnke (1982) found that *Anisophylleaceae* have S-type (starch-containing) plastids, whereas *Rhizophoraceae* have the rare Pvc-type, in which crystalline protein inclusions are found. Further discussion of this and several important chemical characters appear in Dahlgren (this volume).

SYSTEMATIC CONCLUSIONS

A summary of the systematic characters of *Anisophylleaceae* and *Rhizophoraceae* (Table 1) re-

TABLE 2. Characters used in cladistic analysis (Fig. 27). See text for full descriptions of many of the one-word character states.

Character	Condition		
	Ancestral (00)	Derived (01/10)	More Derived (11)
1. Stilt roots	absent	present	
2. Root hairs	present	absent	
3. Phyllotaxy	decussate	bijugate	
4. Stipule vernation	valvate	imbricate	
5. Leaf margin	serrate	entire	
6. Hypodermis	absent	present	
7. Salt-tolerant?	no	yes	
8. Inflorescence	open-branched	fasciculate	
9. Terminal flower	present	absent	
10. Breeding system	hermaphroditic or monoecious	dioecious	
11. Floral laticifers	one layer	radially expanded	idioblastic ¹
12. Petal arista	as laterals	differentiated	
13. Lateral appendages	present	abort	never initiated
14. Petal orientation	reflexed	erect	
15. Androecium	diplostemonous	polyandrous	
16. Hypanthium ²	absent	present	
17. Ovary position	superior	half-inferior	inferior
18. Locule formation	enclosure	schizogeny	
19. Carpels	5	3/many	2
20. Ovules per locule	2	5-8	
21. Receptacle	solid	spongy	
22. Exotegmen	present	vestigial	absent
23. Nucellus	crassinucellate	tenuinucellate	
24. Integument	not vascularized	vascularized	
25. Seed appendage	wing ³	aril ³	none
26. Seeds per fruit	several to many	1	
27. Fruit	dehiscent	baccate	
28. Cotyledons	separate	connate	
29. Cotyledonary node	unilacunar	trilacunar	multilacunar
30. Extra-ovular endosperm	absent	present	
31. Endosperm transfer cells	absent	present	
32. Viviparous?	no	yes	
33. Germination process	by hypocotyl	by endosperm expansion	
34. Seedling establishment	by radicle	by lateral roots	
Autapomorphy		Genus	
35. Multimery		<i>Bruguiera</i>	
36. Explosive pollination system ⁴		<i>Bruguiera</i>	
37. Cotyledonary axillary buds		<i>Bruguiera</i>	
38. Coleorhiza		<i>Bruguiera</i>	
39. Extrastipular glands		<i>Carallia</i>	
40. Androecial appendages		<i>Crossostylis</i>	
41. Stellate pubescence		<i>Pellacalyx</i>	
42. Trichosclereids		<i>Rhizophora</i>	
43. Anemophily		<i>Rhizophora</i>	
44. Multilocellate anthers		<i>Rhizophora</i>	
45. Abortion of first epicotyledonary leaves		<i>Rhizophora</i>	

¹ The idioblastic laticifers or mucilage cells of *Gynotroches* and *Pellacalyx* are here interpreted as derived from the radially expanded ones of other Gynotrocheae. They may actually be instead a cell type *sui generis* within the family, but this has no effect whatever on the cladogram.

² Used here as a perianth/androecium character, independent of ovary position.

³ Separate analyses were carried out with the aril as the ancestral condition, but the resulting trees were essentially topologically equivalent and equally (not more) parsimonious.

⁴ Evolved independently in *Ceriops tagal*; not present in *C. decandra*.

veals virtually no points of agreement. The very few points of vegetative similarity are clearly homoplasies—for example, entire leaves in tribe Rhizophoreae and in Anisophylleaceae. The most frequently cited floral character state common to both families is fimbriate petals (e.g., Tobe & Raven, 1987a), but this also occurs in many dicotyledonous families and is even a diagnostic character of several of these (e.g., Cunoniaceae, Elaeocarpaceae). Moreover, as emphasized above, the petals of Rhizophoraceae have a unique pattern of development and mature morphology and vernation. The ancestral androecial condition in both Rhizophoraceae and Anisophylleaceae is diplostemonous, but this can hardly be regarded as a synapomorphy, as it is found in many other apopetalous dicotyledons. We feel that the overwhelming number of differences in all aspects of growth, anatomy, and reproductive cycle of Rhizophoraceae and Anisophylleaceae make it clear that these two families are not at all closely related. It is to be hoped that the data assembled in addressing this question will also aid in assigning them to their correct phylogenetic positions.

Although more information about the poorly known African genera of Macarisieae will be required before the family can be rigorously revised, a well-supported cladogram (Fig. 27) has been derived from analysis of the 45 characters listed in Table 2. Many other characters that we were unable to study in crucial taxa, or the coding of which could not be satisfactorily resolved, or whose states were unknown in as many as half of the genera, were not included in this preliminary analysis. For the sake of consistency, all anatomical character states noted were derived from our own observations. Computer analysis was carried out using the Phylogeny Inference Package (PHYLIP; Felsenstein, 1985); the PENNY branch-and-bound algorithm was utilized to ensure that all most parsimonious trees were found. Characters were weighted equally and all reversals were permitted. Primarily due to the paucity of characters distinguishing genera of Macarisieae, numerous alternative most-parsimonious trees were found, but all were essentially topologically equivalent and reflected only different placements of the clades and genera of this tribe. Specifying the ancestral condition of the seed appendage as arillate, as would be indicated by comparison with the hypothetical out-groups (Dahlgren, this volume), neither resolves this point nor results in a more parsimonious tree. We emphasize again that more characters from a variety of aspects of the plants are required

in order to elucidate the relationships of the Macarisieae.

A complete character analysis and discussion of generic relationships will be presented elsewhere, but several comments are appropriate here. Tribe Gynotrocheae is clearly paraphyletic and is maintained here and in our synopsis (Juncosa & Tomlinson, this volume) merely for convenience. Despite the occurrence of arils in *Crossostylis*, a character traditionally given much weight, it is clear that this genus is much more closely related to other Gynotrocheae than it is to Macarisieae. It is also evident that *Carallia* is more closely allied to the mangroves than is any other inland genus. In fact, *C. borneensis* shares several additional characters with the mangroves (vascularized integument, frequently single-seeded fruits, complete disappearance of exotegmic cell layer, etc.) that we have conservatively regarded as homoplasies at present. If the extra-stipular glands, the only apomorphy distinguishing the genus, do not occur in all species, then the genus may have to be regarded as paraphyletic, with *C. borneensis* and possibly other species placed further up on the clade leading to Rhizophoreae.

It is instructive to note which characters are homoplastic in Rhizophoraceae. Polyandry occurs in *Kandelia*, *Crossostylis*, and in two subgenera of *Cassipourea*, all independent origins of this character. As described above, this is also reflected in the different modes of development of the additional stamens or, in the case of species of *Crossostylis* not yet studied developmentally, in the positions of those stamens. Condensation of inflorescences also arose at least three times, as did the suppression of later development of the lateral appendages of the petals; this is hardly surprising, considering the minor developmental changes that are involved. Traditionally, the number of carpels or locules and the position of the ovary have been regarded as systematically important, but it is clear that substantial changes in both of these characters have occurred within the Rhizophoraceae. However, the trend from a superior ovary to half-inferior to inferior is reversed only once, in the female flowers of *Gynotroches*. In these, a secondary expansion of the superior portion of the ovary occurs, accommodating the increased number of ovules. Male flowers of the genus also form an ovary and (slightly fewer) ovules, but the ovary is half-inferior. In our judgment, the agreement between the unbiased cladistic analysis and the developmental evidence strongly supports our systematic conclusions.

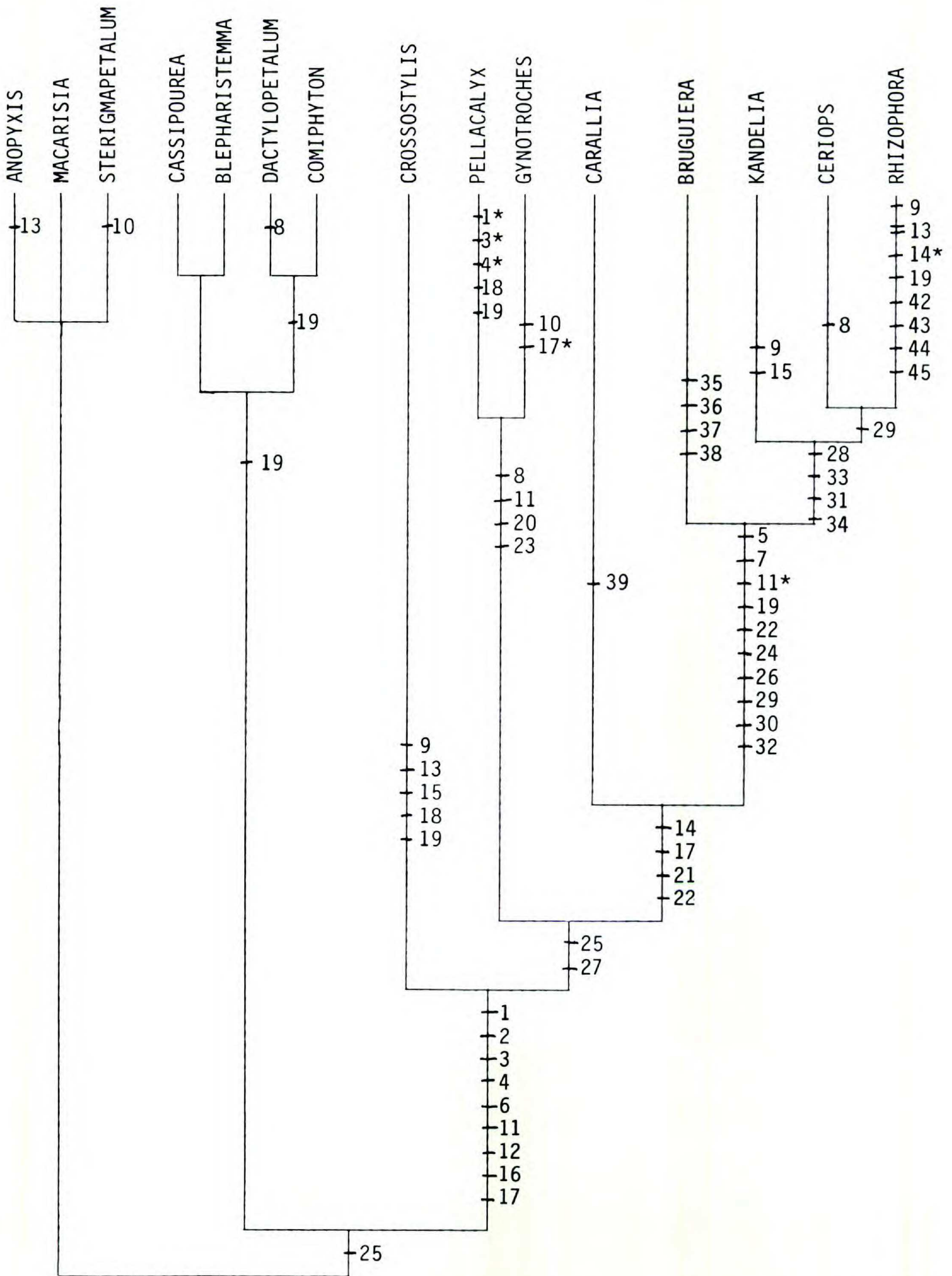


FIGURE 27. Probable phylogenetic relationships of genera of Rhizophoraceae, a most-parsimonious cladogram resulting from analysis of the characters listed in Table 2 by PHYLIP (see text). Alternative equally parsimonious trees reverse the positions of the two basal clades and the genera that terminate them; all these nodes basically represent trichotomies. On the diagram, each mark indicates a one-step change in character state (thus two marks for the exappendiculate petals of Rhizophora); characters noted as changing in more than one place may be multistate or homoplastic or both. Asterisks indicate reversals.

ECOLOGY AND BIOLOGY

The ecological status of mangroves is presented by Tomlinson (1986: 23) as that of species combining the attributes of pioneer species (e.g., early flowering, wide distribution, extended or even continuous flowering and fruiting, short period of dormancy) with attributes of mature-phase species (dense wood, slow growth, large seeds). It is suggested that this is because there is no real succession in the community (although zonation is pronounced) so that individuals have to be both pioneers and climax constituents at different stages in their life span within communities that are inherently unstable. The vegetation itself (mangal) largely shows the characteristics of a pioneer community.

Little is known about the ecology of terrestrial taxa in both families; this makes difficult the search for possible ancestral traits of mangrove taxa within extant rain forest plants.

The following paragraphs outline some of these morphological and biological features, with inevitable emphasis on mangrove taxa, which have been most extensively studied. These plants are unusual in the possibilities they offer, not only for systematic out-group comparison, but for *ecological* out-group comparison, since it is useful to establish those features that occur in unrelated mangrove taxa, i.e., in mangrove members of other families, and which may suggest themselves as features of direct functional significance, and therefore of limited systematic and phyletic value. Aerial roots are an obvious example. In contrast, some features occur in mangrove taxa but not in their terrestrial or ecological relatives.

AERIAL ROOTS

The aerial roots of *Rhizophora* are all initiated from above-ground parts and develop as a series of sympodial loops, which branch aurally only when they are damaged or when the root apex becomes anchored at the end of a loop (Fig. 28). Sympodial branching is adventitious and is of two contrasted kinds. After damage it is distal, i.e., immediately behind the damaged portion, but after anchoring it is proximal, i.e., some distance behind the point of anchorage. A remarkable anatomical transformation occurs in aerial roots as they become submerged distally. Aerial roots have extensive development of trichosclereids, lack aerenchyma, develop secondary xylem, and branch infrequently and adventitiously. Submerged roots lack trichosclereids and other mechanical tissues, develop a lacunose aerenchymatous cortex, have little secondary xylem, and branch abundantly and non-

adventitiously. This kind of root system seems unique to *Rhizophora*. On old trees the trunk-borne roots develop as massive flying buttresses, the trunk base itself being obconical (Fig. 1).

As described in the previous section, *Ceriops tagal* and *Bruguiera sexangula* develop a fluted base formed by the coalescence of clusters of stilt roots that are initiated on the hypocotyl after the seedling has taken root (Fig. 2). This kind of development is also found in the quite unrelated New World mangrove *Pelliciera rhizophorae* (Pellicieraceae) (Tomlinson, 1986). Flutings of this kind seem also to be the maximum extent of aerial root development in *Kandelia*. However, in *Ceriops* and some species of *Bruguiera* an emergent portion of the subterranean root system further develops by the periodic looping of the major horizontal roots, each loop becoming the site of a woody pneumatophore from which branch roots subsequently arise (Fig. 29).

Aerial roots in tropical woody plants have a specific function in supplying oxygen to the submerged roots by the shortest possible pathway in anaerobic, waterlogged substrates. Consequently, such structural variations can be seen as convergences in which developmental modifications result in an identical suite of clearly nonhomologous functional components (Gill & Tomlinson, 1975; Tomlinson, 1986). The functional components always include anchoring and absorption, connecting the separate units horizontally (cable component), and providing for aeration. Consequently, we are provided with a clear picture of the limited value of aerial roots in phyletic analysis. At the same time, this aspect of functional morphology could be a necessary preadaptation in a hypothetical ancestor for the Rhizophoreae. *Kandelia*, which lacks pneumatophores, makes implausible any direct statement about the root system of ancestral mangrove Rhizophoraceae, since it could represent either an ancestral or a derived state. Troll & Dragendorff (1931) denied that aerial roots have a respiratory function and preferred to see them as allowing the trees to root in sediments whose level may fluctuate. The aerating and layering functions are, of course, not mutually exclusive.

WOOD ANATOMY

The relevance of wood anatomy to ecological as distinct from phyletic considerations is again well borne out by a comparison between the mangrove and nonmangrove Rhizophoraceae. The former are uniformly characterized by relatively narrow vessels with scalariform perforation plates, the latter

by wider vessels with partly or exclusively simple perforation plates. One can ascribe the differences in vessel diameters to direct ecological causes because they render the wood of mangroves safer in environments where vessel embolisms are likely to be more frequent as tensions are increased because of the low water potential of sea water (Scholander et al., 1965). Safety is maximized by the production of large numbers of narrow elements (Tomlinson, 1986; Zimmerman, 1983). On the other hand, scalariform perforation plates, whose function is quite unknown, do not seem to have any necessary significance in relation to water stress as suggested by "ecological out-group comparison." Vessel elements in all other true mangroves have simple perforation plates (Janssonius, 1950; Panshin, 1932). Significantly, Sperry (1985) provided experimental evidence that scalariform perforation plates in the palm *Rhapis excelsa* restrict the size of bubbles in recently embolized vessels as they refill with water under positive pressures. Restricting bubble size may facilitate recovery of vessels after water columns are broken during exceptional water stress in any plant. Mangrove Rhizophoraceae could then have a functional advantage not found in their ecological associates from other families.

ARCHITECTURE

Phyllotactic differences between Rhizophoraceae and Anisophylleaceae, so far as they are understood, are but one of a suite of characters that lead to architectural differences of quite a fundamental nature. In the Rhizophoraceae there is a strong tendency toward continuous growth and the expression of Attims's model, whereas *Anisophyllea* suggests rhythmic growth and Massart's model. Continuous growth has been suggested as an adaptive feature in mangrove taxa simply because the tree must remain permanently active metabolically in order to maintain its salt balance (Scholander, 1968; Hallé et al., 1978; Tomlinson, 1986). Trunk axes are therefore monopodial, although they may branch continuously or diffusely. Branching seems always to be by syllepsis (Fig. 31; cf. Wheat, 1981). The branches themselves may then repeat the structure of the parent axis (Attims's model, as in *Rhizophora*) but progressively become plagiotropic by apposition (Fig. 30). Their incipient orthotropy is, however, demonstrated when they are released from apical control; reiteration in *Rhizophora* occurs chiefly by dedifferentiation of existing sylleptic branches.

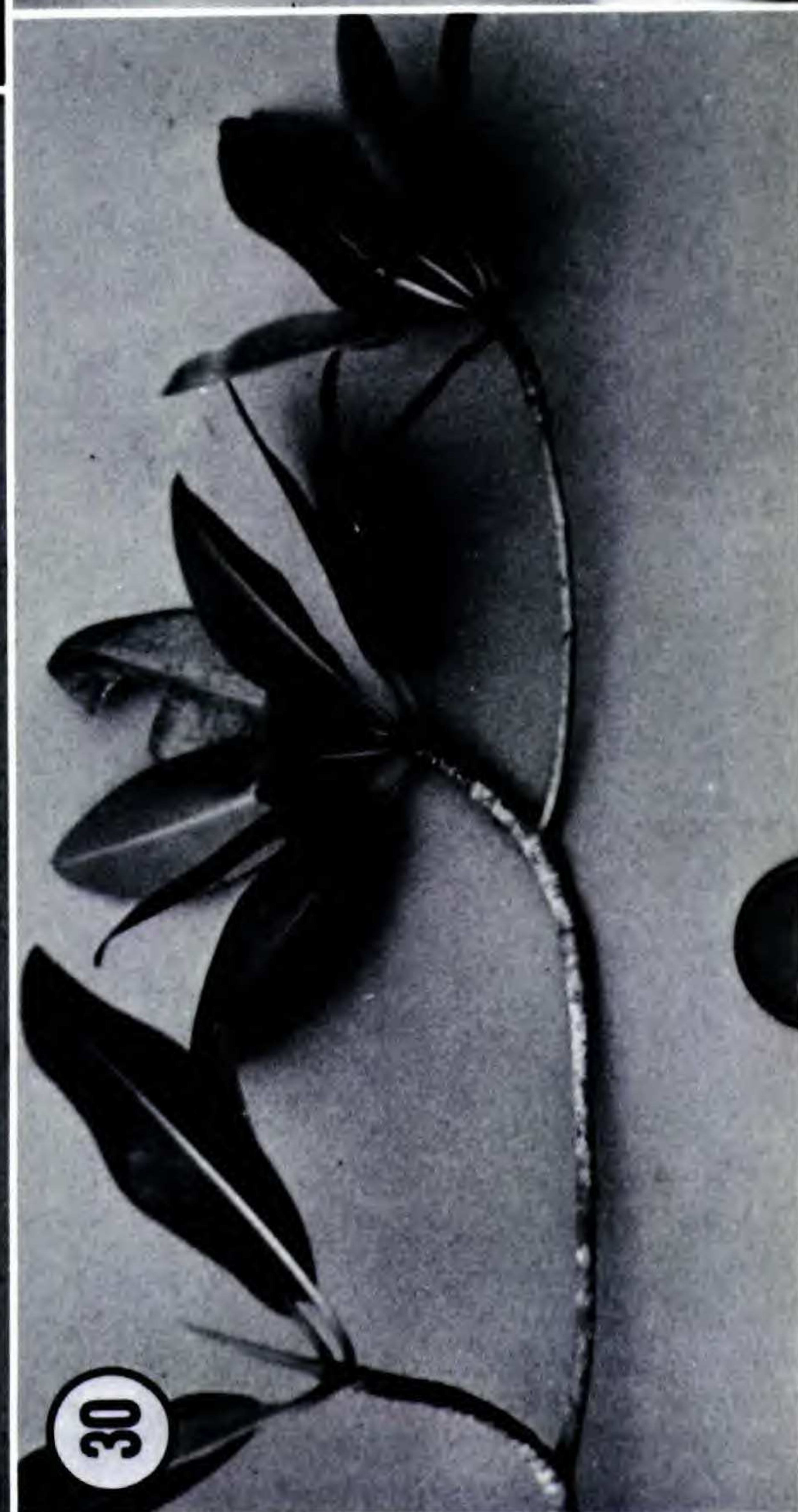
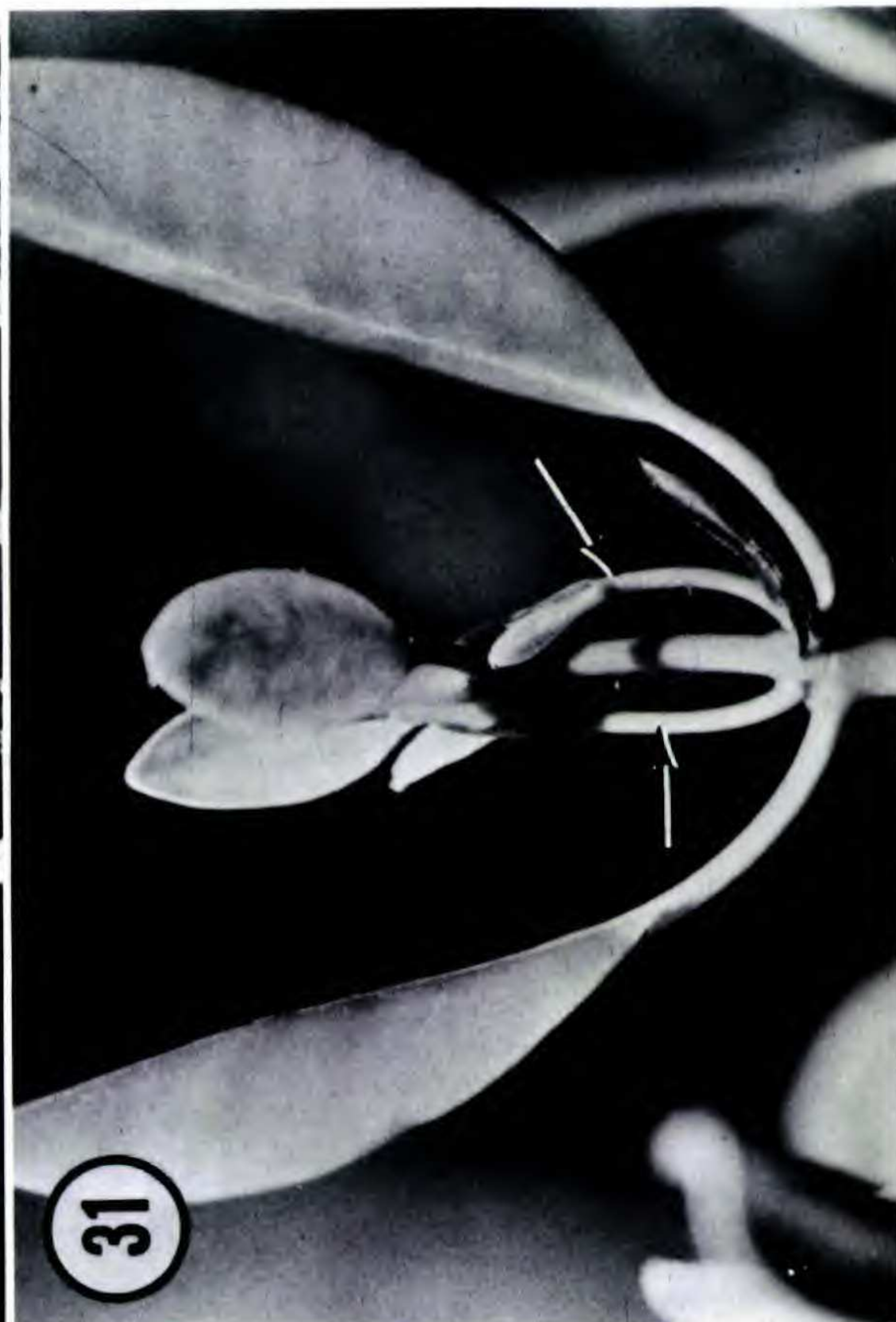
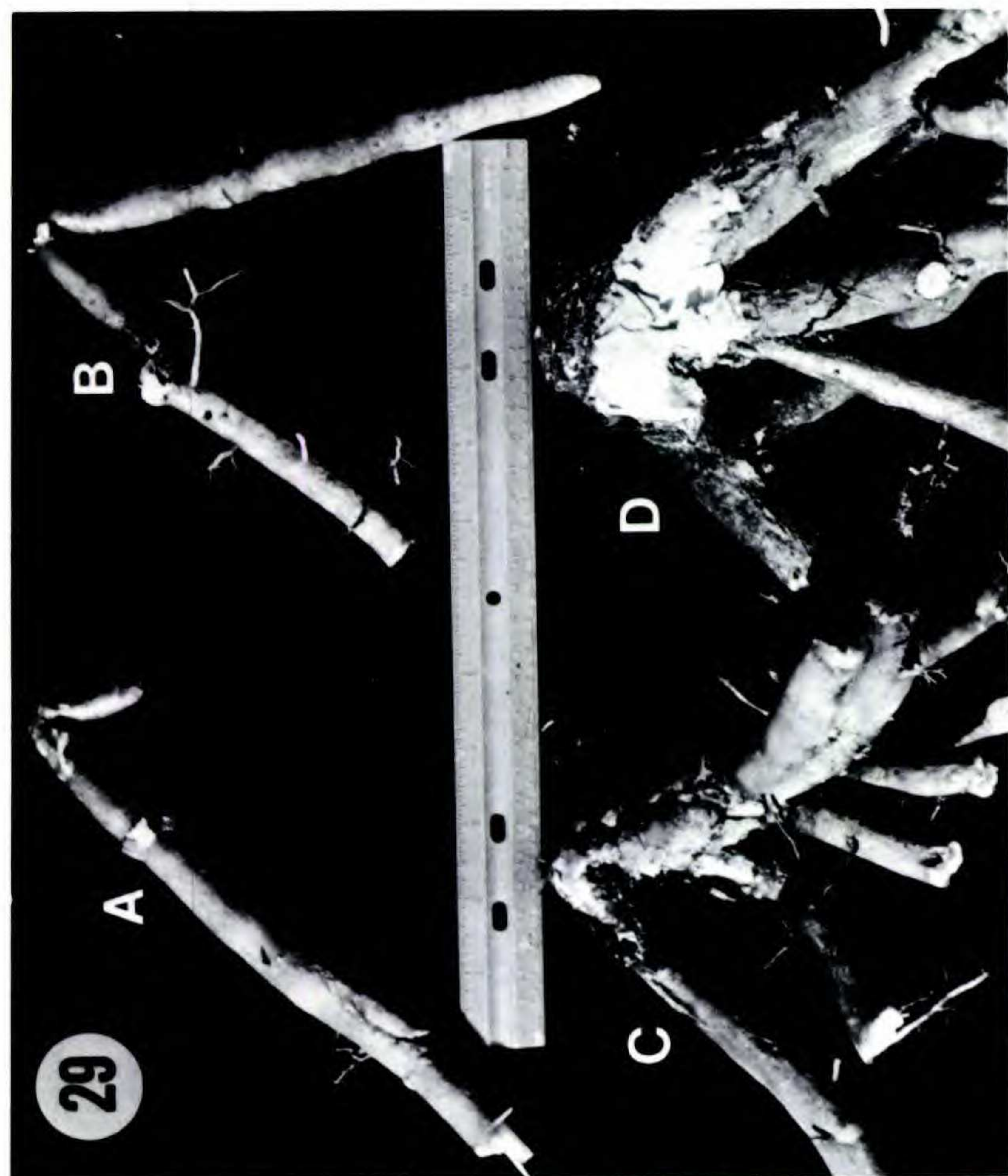
Species of *Bruguiera*, notably *B. gymnorrhiza*,

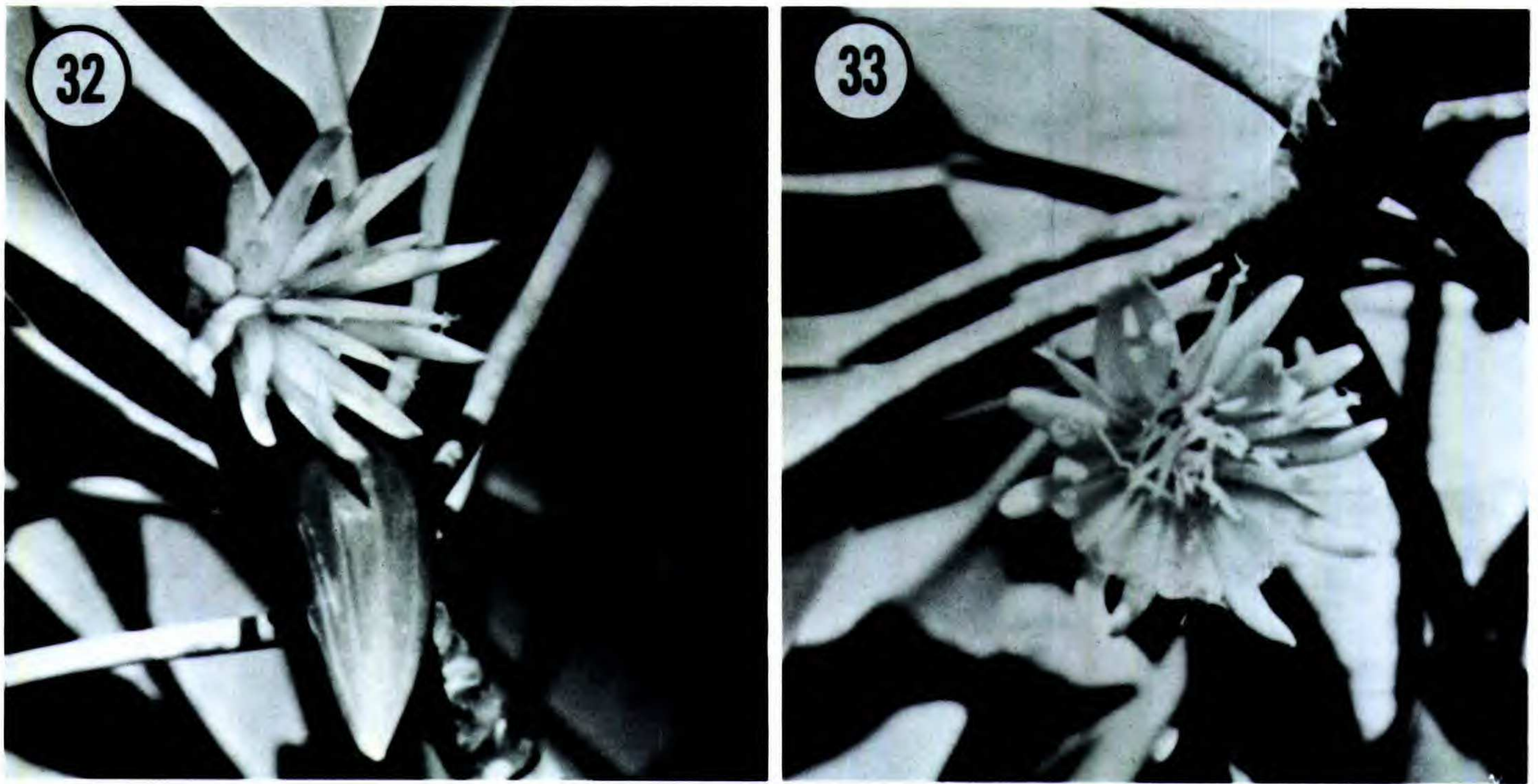
more nearly conform to Aubréville's model, since from inception the branches are plagiotropic by apposition. Dedifferentiation of axes is less common. Although distal branches in trees belonging to these contrasted models all become superficially similar, there is a strong underlying difference: *Bruguiera* tends to remain narrow-crowned, while *Rhizophora* is very plastic in its crown form, especially as lower branches are readily supported by aerial roots. Very likely part of the ecological success of *Rhizophora* as compared with *Bruguiera* lies in this greater plasticity of form. Little is known about the architecture of inland Rhizophoraceae, but superficial study suggests a limited range of crown form comparable to that in *Bruguiera*. *Carallia* and *Gynotroches* seem to conform to Attims's model.

Anisophyllea, in contrast, provides an extreme example of Massart's model (Vincent & Tomlinson, 1983), since the trunk grows episodically, producing pronounced tiers of branches, which are themselves strongly plagiotropic. The trunk axis supports only scale leaves. The differences in phyllotaxis that underlie this contrast have already been mentioned.

Multiple serial buds occur in *Anisophyllea* spp. and some other Anisophylleaceae. The extent to which these are committed at inception to become either reproductive or vegetative branches is unknown. Serial buds also occur in Rhizophoraceae but are more strictly committed at the inception of the first primordia on the axillary apex; the pair of bracteole primordia that form on a future inflorescence apex can be distinguished from leaf primordia that form on a future vegetative apex. It should be emphasized that in most Rhizophoraceae that we have studied, vegetative branching is by syllepsis, additional vegetative "reserve" buds may be formed as part of a primary branch complex, but their further development is very limited (Wheat, 1981). In both inland and mangrove genera, when the plant is in reproductive condition, an inflorescence develops in the axil of each leaf of a pair, and, at least on vigorously growing shoots, a single vegetative bud develops above this, although it is often not evident even with a hand lens. In adult *Rhizophora*, reiteration can occur from these residual buds, but more usually reiteration is the result of dedifferentiation of existing branches. Adventitious buds, however, do occur on the hypocotyl of damaged seedlings (Larue & Muzik, 1954; Gill & Tomlinson, 1969).

In summary, we recognize that Rhizophoraceae and Anisophylleaceae differ in architecture and reiterative ability in ways that support their seg-





FIGURES 32, 33. *Floral mechanism in Bruguiera gymnorhiza*.—32. Flower before being tripped; stamens are enclosed under tension by the petals.—33. Similar flower after being tripped; petals spring open, releasing the stamens and pollen explosively. Stamens are now visible at center of flower.

regation as two families. If this discussion seems imperfectly formulated, it is simply because the problem of morphological plasticity in woody plants of the tropics itself is a subject that remains little understood, despite its considerable ecological importance.

FLORAL MECHANISMS

Understanding of floral structure and development stands in an interesting relationship to our knowledge of floral mechanism, which is fairly complete for the mangrove taxa, from the work of Tomlinson et al. (1979) and Kondo et al. (1987), but is scarcely investigated for either terrestrial Rhizophoraceae or Anisophylleaceae. In the Rhizophoreae there is an initial contrast between *Rhizophora*, which is wind-pollinated, and the other genera, which are animal-pollinated. Evidence for wind pollination comes from floral mechanism, pollen-ovule ratios, dispersibility of pollen, and infrequency of insect visitors, even though the flowers do not display a conspicuous wind-pollination syn-

drome as it is familiarly understood for temperate trees. Animal pollinators of other genera include birds, bees, moths, and butterflies, at least, with each species or group of species visited by a particular type of flower visitor. Floral specialization involves a very distinctive explosive mechanism that physically projects the light pollen onto the visitor but only when the mechanism is tripped by the visitor (cf. Figs. 32, 33). Differences in the biotic interaction relate to differences in flower size, orientation, and attractant (nectar and odor). *Ceriops decandra* and *Kandelia* lack any specialized mechanism and seem to be pollinated by rather generalized visitors. Of interest is that *Ceriops tagal* and *C. decandra* are strongly contrasted in their floral mechanism. The existence of light powdery pollen in the taxa with animal pollination is an example of the way in which pollen characteristics may be misleading about the method of pollination; most animal-pollinated plants have heavy, sticky pollen. In the Rhizophoreae one may speculate that this pollen type is a preadaptation for wind pollination in *Rhizophora*, which represents

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FIGURES 28–31. *Root and branch development in Rhizophoreae*.—28. Development of aerial root system of *Rhizophora*; branch roots arise from the arches after the main apex enters the substrate (Queensland, from a transparency by A. M. Gill).—29. Development of knee roots in *Ceriops tagal* (Philippines, from a transparency by A. M. Gill). Successive stages are indicated A–D. Similar development occurs in *Bruguiera* (see Fig. 2).—30. Older branch of *Rhizophora mangle*, which has become plagiotropic by apposition.—31. Sylliptic branching (arrows) in *Ceriops tagal*; branches are elongating even before stipule has fallen from the node.

a derived condition, and is itself an adaptation to animal pollination by the distinctive explosive projection of pollen. Flower orientation itself provides contrast with reference to classes of visitor. Small-flowered species of *Bruguiera* have erect flowers, suitable for the approach from above of small, delicate-winged visitors, such as butterflies; large-flowered species of *Bruguiera* have pendulous flowers on recurved pedicels and are approached from below by large visitors like birds. There is evidence that pollination can occur in conditions of autogamy, allogamy, and geitonogamy, but none for apomixis (Kondo et al., 1987).

The general ecological conclusion is that this group of related mangrove plants partitions the available pollinator resource by adopting either different mechanisms, or, where there is a common mechanism, by varying it to suit different types of pollinator.

CONCLUSIONS

The phyletic and systematic conclusions of the various contributors to this symposium are drawn from an examination of a remarkable diversity of characters, ranging from features of gross morphology to ultrastructural details of sieve-tube plastids. Consciously or unconsciously there is a good deal of weighting of these characters; consciously because there can be bias towards acceptance of a character state if it agrees with a pre-existing position, unconsciously because a single biological character (e.g., wind-dispersed seeds) may be reflected in several morphological characters (dehiscent fruits, winged seeds, thin seed coat). Rarely is a character sufficiently understood at a functional level for the bias to be rational. The taxonomist will emphasize that it is impractical to consider the possible biological significance of all attributes of a character in making systematic hypotheses, but the consequences of this restriction should at least be understood. The more information one has about a feature used in systematic analysis, the more likely that its systematic or phyletic significance can be correctly assessed. Subjectivity is an inevitable consequence of the empiricism of systematic methodology—the papers in this symposium are replete with examples—and any claim of objective neutrality is particularly inappropriate where the evolutionary polarity of character states is continually invoked. There should be some appreciation of what may be termed “biological” attributes of characters if they are to be manipulated successfully.

Within this broad spectrum of attributes, specific

attention needs to be given to three classes of information: correlation among characters; functional aspects of characters; developmental history of characters, particularly at the primordial level.

An understanding of the way in which seemingly different characters are correlated is necessary since an apparent complex that may or may not be structurally connected may all be subsumed as a single character if the interdependence is appreciated. For example, phyllotaxis, stipular morphology and nodal anatomy are interlinked; thus, aspects of nodal vasculature may be a direct expression of phyllotaxis, as in the presence or absence of split laterals, distinguishing Rhizophoraceae from Anisophylleaceae. More subtle physiological connections need to be sought, as in the relation between leaf succulence and salt-excluding mechanisms in Rhizophoraceae.

The contrast between mangrove and terrestrial taxa in such features as root morphology, leaf anatomy, wood structure, and embryo development could well be cited as characters with little systematic weight because their functional attributes are at least perceived, if not totally understood—they are the “Anpassungsmerkmal” of Schimper. It is well established that the tribe Rhizophoreae is an advanced group, even though a diagnostic feature is the presence of scalariform perforation plates in its wood. An evolutionary scenario sees this simply as the retention of a putatively primitive character. If this is true, it is surely helpful to know why it has been retained. If the preferred explanation of the function of scalariform plates in restricted air-bubble size in embolized vessels is accepted, we can appreciate its occurrence in a more informed way.

Developmental information may simply add to the range of characters made available, an attribute that strongly justifies embryological study (cf. Tobe & Raven, 1987a, b), but it can also clarify structural, functional, and correlative attributes; for example, floral development suggests that pleiomery is derived in the Rhizophoraceae. The best example is provided by *Kandelia*. Here the feature is related to a rather unspecialized floral mechanism that may be derived, not an ancestral feature. Currently we have no evidence for a specialized pollinator group in this genus. Comparative study of embryo development shows a trend of modification leading from epigeal germination to vivipary, with *Bruguiera* the least specialized within the viviparous group. “Vivipary” becomes more useful as a systematic character when viewed developmentally, even though we do not understand its functional significance. Developmental study may also reveal

the extent of convergence, in which superficially similar structures show contrasted developmental pathways; the diversity of root systems is a very gross example.

These examples relate to "primordial development" (Tomlinson, 1982); "ontogenetic development" provides an independent set of attributes. The distribution of axes with contrasted kinds of phyllotaxis in Anisophylleaceae clearly has an ontogenetic component that is still incompletely explored. Once it has been done and its correlation with stem vasculature worked out, we are likely to be in a position to make evolutionary statements, because some of the phyllotactic patterns in this species are clearly derived, as indicated by their uniqueness.

Inevitably these considerations of "character analysis" to which we have drawn attention may lie in the realm of "consummations devoutly to be wished" as far as practicing systematists are concerned. Nevertheless we hope that investigations of functional, developmental, and correlative attributes can be seen to play a central role in systematics.

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